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Multiscale factors structuring diversity in taxa, traits and evolutionary units of spiders in tropical environments

Kaïna Privet

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Spécialité : *Écologie et Évolution*

Par

Kaïna PRIVET

« Multiscale factors structuring diversity in taxa, traits and evolutionary units of spiders in tropical environments »

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TABLE OF CONTENTS

Glossary.....	1
Introduction.....	5
Study of diversity patterns and the processes behind them	5
Diversity or diversities?	5
Patterns and processes of diversity	7
The three main components of diversity	10
Spiders as a model for studying diversity	16
The evolutionary and ecological success of spiders.....	16
Spider taxonomy	18
Status of the trait-based approach in spiders.....	18
Spider phylogeny.....	21
Known diversity patterns and processes in spiders.....	22
Study of the diversity of spiders in tropical environments.....	24
Hotspots of diversity	24
The difficulties of studying the diversity of tropical spiders	24
Objectives and thesis organization	27
Part I: Factors structuring taxonomic diversity of tropical spiders	29
CHAPTER.1 Efficiency of Pitfall Trapping vs. Nocturnal Hand Collecting in Assessing Soil-Dwelling Spider Diversity along A Structural Gradient of Neotropical Habitats	31
Abstract	31
Introduction.....	32
Materials and methods	33
Results	35
Discussion	38
Acknowledgments	40
Funding.....	41
References.....	41
Supplementary Materials	44
CHAPTER.2 Spider assemblage structure in a Neotropical rainforest-inselberg complex: ecological and methodological insights from a small-scale intensive survey	47
Abstract	47
Introduction.....	48
Materials and methods	50
Results	53
Discussion	57

Acknowledgements	62
References.....	62
Supporting Information.....	67
Part II: Complementarity of traits et taxons for understanding diversity patterns of tropical spiders.....	73
CHAPTER.3 Comparative patterns in taxonomic and functional spider diversities between tropical vs. temperate forests.....	75
Abstract	75
Introduction.....	76
Methods	77
Results	79
Discussion	81
Acknowledgments	83
References.....	84
Supporting information	88
CHAPTER.4 Complementary of taxon- and trait-based metrics to understand tropical patterns of diversity –A case study using spider assemblages of contrasted neotropical forests habitats	93
Abstract	93
Introduction.....	94
Material and methods.....	96
Results	100
Discussion	108
Acknowledgements	110
References.....	111
Supplementary Materials.....	121
Part III: Describing and understanding tropical spider diversity using a phylogenetic approach: the case of Hawaiian wolf spiders.....	123
CHAPTER.5 Phylogenetic relationships among Hawaiian wolf spiders suggest recent radiation driven by the adaptation to different environments.....	125
Abstract	125
Introduction.....	126
Materials and methods	132
Results	140
Discussion	148
Acknowledgements.....	154
References.....	154

Supplementary materials	163
General discussion and perspectives	183
General discussion: habitat plays a role in tropical spider diversity.....	183
Research perspectives.....	186
Further investigations of the assembly rules of tropical spiders.....	186
Rethinking sampling in tropical environments: the need to use a set of sampling methods in standardized protocols.....	188
Importance of taxonomy.....	189
Towards the development of a trait-based approach adapted to tropical ecosystems	189
Using NGS to resolve complicated evolutionary relationships	190
Conclusion	190
References.....	191
Appendix.....	214
APPENDIX.1 Towards establishment of a centralized spider traits database	214
Abstract	214
Introduction.....	215
General database benefits	216
Benefits of a spider traits database	217
Logistics of a traits database	218
Additional challenges for a spider traits database.....	221
Potential research that would become feasible with a spider traits database	221
Outlook.....	222
Acknowledgements.....	223
Litterature cited.....	223
APPENDIX.2 The World Spider Trait database (WST): a centralized global open repository for curated data on spider traits	228
Abstract	228
Background & Summary.....	229
Methods	230
Data Records	234
Technical Validation	237
Usage Notes.....	238
Code Availability.....	239
Acknowledgements.....	239
References.....	239
Supplementary information.....	242

APPENDIX.3 New species of Hypaeus Simon (Araneae: Salticidae: Salticinae: Amycini) based on integrative taxonomy.....	254
Abstract	254
Introduction.....	255
Material and Method	256
Results	259
Acknowledgements.....	266
References.....	266
APPENDIX.4 Non-native spiders change assemblages of Hawaiian forest fragment kipuka over space and time.....	270
Abstract	270
Introduction.....	271
Materials and methods	271
Results	272
Discussion.....	275
Acknowledgments.....	276
References.....	276
Curriculum Vitae.....	278

GLOSSARY

Assemblage: taxonomically related group of populations of species that are found together in space (Stroud *et al.* 2015).

Biogeography: the study of the patterns of distribution of diversity in organisms and ecosystems, in space and time, and the factors that determine these patterns. It is a field of study at the intersection of systematics, ecology, evolution, and phylogeography.

Community: a group of organisms that live together in space and time and interact with each other (Stroud *et al.* 2015).

Diversity: the variety of living things in terms of taxonomic units, traits, and evolutionary units, at scales of space and time (Pavoine & Bonsall 2011).

Diversity patterns: arrangement of diversity components (i.e., taxa, traits, and evolutionary units) at a scale of life, e.g., variation in taxonomic diversity between communities. There are two types of patterns: spatial and temporal. These patterns are the result of ecological and evolutionary processes (Scheiner 1992, Pavoine & Bonsall 2011).

Community Ecology: the study of patterns of diversity, abundance, and composition of species in communities and the processes that drive these patterns and the functioning of communities (e.g., biotic interactions) (Wilco & Verbek 2011).

Factors: each of the parameters or components of the environment that affect the organisms and the functioning of the ecosystem and therefore the distribution, abundance, and evolution of the biocenosis. They can be biotic (e.g., trophic relationships, competition) or abiotic (e.g., chemical and physical components of the environment such as climate, topography) (Gilpin 1996). The factors influence the processes that determine diversity patterns.

Habitat filtering: process driving the patterns of diversity through the exclusion of species whose trait combinations are inappropriate for the given abiotic and biotic conditions of a habitat (Keddy 1992).

Hyperdiversified (or megadiversified): "highly diverse". A term used for a living unit (group, taxon, assemblage, community) or an area (habitat, environment, country) and which refers to the quantity of the unit (often species). First used at a conference on biodiversity (Smithsonian Institution, Washington) to describe countries with at least 5,000 endemic species (Australian State of the Environment Committee 2001).

Integrative taxonomy: the science that aims to delineate the units of diversity of life (e.g., species, genera, families) from multiple and complementary perspectives such as

phylogeography, comparative morphology, population genetics, ecology, development, behavior (Dayrat 2005).

Morphospecies: groupings of similar individuals, categorized on the basis of external morphological characteristics, without recourse to taxonomy (Oliver & Beattie 1996b).

Niche: set of environmental conditions, i.e. physical (e.g., habitat, temperature, humidity, pH) and resources (e.g., particular type of food, food size), from which stable populations can be maintained (Hutchinson 1957).

Parataxonomy: an approach that consists of grouping organisms to 'species' based on external morphological characteristics, without considering taxonomy. These groups are called morpho-species (Krell 2004, Abadie *et al.* 2008). This approach is used in cases where literature and/or specialists in the group of interest are not consulted, available or existing.

Processes (at the origin of diversity patterns): processes

- Whose intensity varies according to changes in the environmental factors
- Which influence secondary processes (e.g., speciation rate, degree of specialization, niche extent or coverage, community structure) differently in different environments

These processes are assumed to control the observed diversity patterns directly or indirectly. A distinction is made between the processes that cause diversity, which are the processes that influence diversification, and the processes that cause patterns of diversity, which influence its structuring in space and time. Processes can also be categorized according to whether they are deterministic or stochastic, ecological or evolutionary (Weiher & Keddy 2001)

Deterministic processes: any process that involves non-random, niche-based mechanisms. E.g., habitat filtering, competition, predation (Weiher & Keddy 2001).

Stochastic processes: any process that gives rise to patterns of diversity, abundance, and species composition that cannot be distinguished from chance alone. E.g.: genetic or ecological drift, dispersal (Hubbell 2001).

Ecological processes: the interactions between individuals of the same or different species and between them and their environment, which determine the dynamics of populations, communities, and ecosystems on an ecological timescale, usually over a few generations (Bartolo *et al.* 2018). E.g., climatic processes, productivity, the effect of habitat on diversity, interactions between organisms.

Evolutionary processes: any process leading to genetic changes in populations, resulting in divergence and persistence of lineages on an evolutionary time scale,

usually extending over many generations (Nature Education 2022). E.g., selection (sexual and natural), genetic drift, mutations, gene flow.

Species: lineages of populations or metapopulations that evolve separately (De Queiroz 2007).

Traits: morphological, anatomical, biochemical, physiological, or phenological characteristics measurable at the individual level that reflect the result of evolutionary processes and community assembly responding to abiotic and biotic environmental constraints (Violle *et al.* 2007, Kattge *et al.* 2011).

INTRODUCTION

Study of diversity patterns and the processes behind them

Understanding the origin of patterns of biological diversity is one of the major challenges of modern ecology. Entire fields of ecology are dedicated to this, whether to understand the patterns of diversity of organisms and the processes responsible for them at the community level (community ecology) or at broader scales of time and space (phylogeography, biogeography). In this first part, we focus on defining the concept of diversity, presenting the state of knowledge on diversity patterns and processes, and describing the main components of diversity.

Diversity or diversities?

Definition

Diversity is a rich concept, with many possible definitions (Harper & Hawksworth 1994, DeLong 1996). In its broadest form, diversity (see **box 1** for difference with biodiversity) can be seen as the variation or heterogeneity of living things, at all scales and levels of organization: from variations between individuals to the infinite complexity constituted by the assemblage of countless communities that make up the biosphere (Faith 2016). This includes for example specific, functional, genetic, and phylogenetic diversity. There are therefore many components of diversity and it is impossible to describe 'diversity' as a simple order of magnitude (Gaston & Spicer 2013). Yet the word diversity has very often been used as a synonym for species diversity, and the other components have been less explored in ecology (Colwell 2009, Pavoine & Bonsall 2011). Advances in recent years, e.g., in terms of producing molecular phylogenies or studying traits, have greatly improved our understanding of the importance of considering phylogenetic relationships and functional traits in diversity (e.g., Violle *et al.* 2007, Cavender-Bares *et al.* 2009, Mouquet *et al.* 2012). Diversity was then redefined as "a complex, multifaceted concept that includes scales of space and time, and entities such as species, traits and evolutionary units" (Pavoine & Bonsall 2011). We will elaborate on these components (species, traits, and evolutionary units) later (see section **The three main components of diversity**, page 10 and following).

Box 1. Difference between diversity and biodiversity

Biodiversity is a neologism that appeared at the Washington Forum in 1986 (but see previous use in Faith 1970) and was internationalized in 1992 at the Earth Summit in Rio. The concept of biodiversity is a scientific, social, and political construction and has highlighted the need to collaborate in the face of the environmental crisis (Charvolin & Ollivier 2017). This concept, therefore, does not only include the diversity of living things, but also the value of this diversity and the interactions of humans with living things (Toepfer 2019). It, therefore, links many disciplines such as biology, bioethics, philosophy, economics, law, and politics. These different disciplines actually study different things (Meinard *et al.* 2019). For example, specific, functional, or phylogenetic diversity is studied in Ecology; naturalness or perceived diversity in environmental economics and sociology. Also, Toepfer (2019) suggests considering 'biodiversity' as an absolute metaphor like 'life', 'time' or 'world', thus explaining that the term has no fixed definition as it mediates between various contexts and disciplines. As this thesis is set in a scientific ecology framework, we prefer to use the term 'diversity', as we will not discuss other facets of biodiversity and do not want this work to be considered a scientific approach to 'biodiversity' (see Sarkar 2019 for a definition of the scientific approach of biodiversity).

Scales of diversity

There are many **scales of organization of living organisms** at which diversity can be studied, e.g., individual, population, community, meta-community. Among these, the community scale is one of the most widely used in diversity studies. Communities are defined as groups of organisms that live together in space and time and interact with each other (Whittaker 1975). In this thesis, the use of the term assemblages will be preferred, defined as groups of taxonomically related organisms of species populations that are found together in space and time, without the notion of biotic interactions between them (as we have not studied them), although they may exist (Fauth *et al.* 1996, Magurran 2004, Stroud *et al.* 2015).

Diversity is also partitioned at **spatial scales** (Whittaker 1960) (**Figure 1**). Taxonomic, trait and phylogenetic diversities can be studied (1) at the local scale of an assemblage or habitat, termed alpha (α) diversity, (2) between local assemblages or habitats, termed beta (β) diversity (see also zeta (ζ) diversity, which includes the different diversity metrics between habitats, Hui & McGeoch, 2014), (3) at the regional or meta-community scale (a set of local communities linked by dispersal), called gamma (γ) diversity. These components were later reused to highlight the importance of temporal partitioning (between years, decades, and centuries) of diversity (Pavoine *et al.* 2009, Pavoine & Bonsall 2011, Mushet *et al.* 2019).

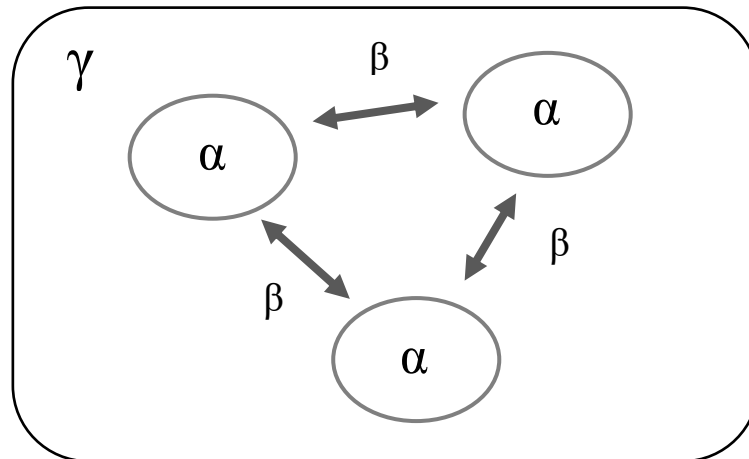


Figure 1: Spatial distribution of diversity. Gamma diversity (γ) is the diversity of all assemblages at the regional scale, alpha diversity (α) is the diversity of an assemblage at the local scale and beta diversity (β) is the diversity between assemblages. From Daly et al. 2018.

Patterns and processes of diversity

Diversity patterns are spatial or temporal arrangements of diversity components (i.e. species, traits, and evolutionary units) at a scale of life, e.g., variation in species diversity between assemblages (Scheiner 1992). The processes that drive diversity patterns in communities are processes such as competition, predation, or habitat filtering, which vary in intensity depending on the environment and directly or indirectly determine the observed diversity patterns (Osman & Whitlatch 1978). We need to describe and understand diversity patterns well to make inferences about the processes that cause them.

Main diversity patterns

Diversity patterns have been best described for species diversity. This component of the diversity of living organisms is heterogeneously distributed among taxa and on the surface of the planet.

Around 1.43 million species of eukaryotes have been described within the estimated 10.95 million species (Mora *et al.* 2011). About 1% of these species are vertebrates, 10% are plants and 90% are invertebrates (May 2010), with half of the invertebrates being arthropods (Chapman 2009).

At the surface of the planet, diversity varies according to spatial factors such as latitude, surface area, remoteness, or ecological and environmental factors such as biological productivity, altitude, habitat heterogeneity, habitat complexity, or disturbance (Ricklefs & Schluter 1993). Patterns of species diversity have been extensively synthesized (Pianka 1966, Ricklefs & Miller 1999, Willig *et al.* 2003, Vellend 2010), and here we will only mention some of them for which knowledge also exists for traits and evolutionary units (measured by phylogenetic diversity).

At a broad scale, there is a latitudinal increase in species diversity in most organisms, reaching a maximum in the tropics (Willig *et al.* 2003). It is known, for example, that tropical forests may contain ten times more tree species than forests of similar biomass in temperate regions (Latham & Ricklefs 1993) and between 2.1 and 8.4 times more terrestrial arthropods (Basset *et al.* 2012) (**Box 2**). This pattern is also found when considering phylogenetic diversity, e.g., Fritz & Rahbek (2012), Smith *et al.* (2017), Massante *et al.* (2019) in amphibians, birds, and plants, respectively. Conversely, trait diversity does not always follow this latitudinal gradient. For example, Schumm *et al.* (2019) found that tropical faunas of marine bivalves and land birds are more trait-rich but less regular than those of temperate regions. Cardoso *et al.* (2011b) showed that trait richness in spiders is not always higher in the tropics than in temperate regions and Lamanna *et al.* (2014) that trait diversity in trees is higher in temperate environments.

At a more local scale, diversity varies along with environmental gradients as well as between habitats depending on their productivity, structure (heterogeneity, complexity), isolation, altitude, or physical conditions (Ricklefs & Miller 1999). For example, spider species diversity is higher when the vegetation structure is more heterogeneous (in terms of stem height) (Greenstone 1984). Plant species diversity is strongly related to soil pH (Pärtel 2002).

To date, there is no synthesis of diversity patterns in species, traits, and evolutionary units. However, empirical observations suggest that diversities scale differently depending on whether one considers species, traits, or evolutionary units. Attempts to generalize diversity patterns to all lineages of life (e.g., the latitudinal diversity gradient Willig *et al.* 2003) have shown that patterns differ between groups. Studies of local patterns show that patterns vary between regions (Pärtel 2002). Therefore, there is a need to continue to describe diversity patterns, both at local and regional scales, in all groups, taking into account other components of diversity to re-evaluate the frequently described patterns of species diversity.

Box 2. Terrestrial arthropods of tropical forests: why study spiders?

Most species of eukaryotes are terrestrial arthropods (Chapman 2009), and most terrestrial arthropods are found in tropical forests (Erwin 1982). In many ways, tropical forests represent the least known of the diverse communities inhabiting terrestrial ecosystems (Ramade 2003). Some consider tropical forests to be "the last unexplored frontier of the biosphere" (Wilson 1992).

Studies that have estimated the diversity of tropical arthropods are based on the correlation between the species diversity of plants and phytophagous animals (e.g., Erwin 1982, Ødegaard 2000, Novotny *et al.* 2002). However, there is a lack of knowledge on the relationship between plant diversity and non-phytophagous animals (e.g., generalist or specialist carnivores, omnivores) (but see Basset *et al.* 2012, Dinnage *et al.* 2012). Within arthropods, most hyperdiverse groups seem to owe their diversity to hyperdiversification of feeding strategies (e.g., Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera, and Mites are polyphagous groups) (Rainford & Mayhew 2015). Thus, estimates of tropical arthropod diversity based on plant-animal phytophagous relationships are biased.

Among the hyperdiverse arthropod groups in tropical forests, spiders are one of the only groups that are exclusively predatory (Birkhofer & Wolters 2012). Studying the diversity of tropical spiders should therefore test the relationships between diversity patterns of plants and predatory arthropods.

Main processes responsible for diversity patterns

Current diversity is the product of ecological and evolutionary processes, which may be stochastic (i.e. neutral) or deterministic (i.e. niche-related), and their interactions.

From a **deterministic ecological process** perspective, biotic and abiotic factors influence diversity patterns (Weiher & Keddy 2001, Maire *et al.* 2012) via niche differentiation (MacArthur & Levins 1967) and habitat filtering (Keddy 1992), respectively. Habitat filtering limits the establishment of species that are unable to tolerate the abiotic conditions of a given habitat, resulting in the survival of species with similar ecological attributes in a given area (Keddy 1992). Competitive interactions can reduce the coexistence of species that share similar niches (MacArthur & Levins 1967) or enhance competitive hierarchies between species (Chesson 2000, Kunstler *et al.* 2012), resulting in niche differentiation through trait displacement: through spatial and/or temporal partitioning of species with similar ecological attributes (Diamonds 1975, Gotelli & McCabe 2002). These deterministic processes apply at different spatial scales such as local or regional scales (Chase & Myers 2011). At the same time, assemblages are influenced by more **stochastic ecological processes** such as colonization, random extinction, and ecological drift (Chase & Myers 2011).

The role of **evolutionary processes** in determining diversity patterns at the assemblage level has been less studied than that of ecological processes (Gillespie 2004). One evolutionary process, **adaptive radiation**, has been proposed as the main contributor to global diversity (Simpson 1953, Schluter 2000). Adaptive radiation is a process by which organisms rapidly diversify from an ancestral species into a multitude of different new ecological forms (Gillespie *et al.* 2001). It is therefore a complex process of speciation driven by ecological factors (e.g.,

ecological adaptation) (Gavrilets & Vose 2005, Gillespie *et al.* 2020). The best known adaptive radiations come from isolated archipelagos or pseudo-islands (e.g., lakes) (Gillespie *et al.* 2001) and are often spectacular, e.g., the 15 species of Galapagos finches, known as 'Darwin's finches' (Lack 1983, Lamichhaney *et al.* 2015), the species of Cichlida fishes of Lakes Tanganyika (208 species), Malawi (800-1000 species) and Victoria (more than 200 species) in South Africa (Johnson *et al.* 1996, Galis & Metz 1998, Seehausen *et al.* 2008, Ronco *et al.* 2020), the approximately 1000 species of Drosophilidae of the Hawaiian archipelago (Carson & Kaneshiro 1976).

Linking patterns of diversity with the processes behind them has been identified as one of the great challenges of ecology (Vellend 2010). The task is daunting at the local scale and the rules of assemblages seem so specific (i.e. different processes determine the diversity of different taxa, and sometimes between contexts for the same taxon) that some speak of the 'black box' of community ecology to refer to the links between patterns and processes (Vellend 2010), as well as the link between ecological and evolutionary processes (Gillespie 2016).

The three main components of diversity

Diversity in species, traits, and evolutionary units are linked. In this section, we detail these three components of diversity and present the interest of taking them into account in a combined manner to determine diversity patterns.

The taxonomic approach of diversity

Species are among the basic units of diversity and have long been considered the most important component of diversity (Claridge *et al.* 1997, Hohenegger 2014). This importance is related to the fact that species is used as the basic taxonomic unit in systematics (Linné 1735) and evolutionary biology (Barraclough 2019). It has therefore long been considered the fundamental level in ecology (De Queiroz 2005). The study of the species diversity of organisms has made it possible to highlight numerous patterns such as the latitudinal gradient of diversity, the area-species relationship, or successions along environmental gradients. It has the advantage of being easily understandable and accessible if the species studied are known. However, the species diversity approach also has its limitations.

The first limitation is related to the difficulty of **defining and delimiting species**. Biologists have historically used different concepts of species, some of which are partially incompatible (Mayden 1997, De Queiroz 1998, 2007). A unified and simplified definition has been proposed (Giray 1976, Dayrat 2005, De Queiroz 2007) in which species are "separately evolving population lineages or metapopulations". Taking this definition into account, an integrative approach to species delimitation (integrative taxonomy) has emerged that takes into account phylogeography, comparative morphology, population genetics, ecology, development, and behavior (Dayrat 2005). The integrative taxonomy approach requires a good knowledge of the

organisms studied. However, this is not always the case (e.g., hyperdiverse arthropod groups in tropical forests or isolated ecosystems), and it is, therefore, necessary to use parataxonomic approaches to estimate diversity. In the current thesis, we prefer to talk about taxonomic diversity rather than species diversity as the organisms we study are not described yet.

The second limitation of species diversity is **its measurement**. Species diversity is usually represented by species richness alone: the number of species (Humphries *et al.* 1995, Colwell 2009). However, species richness is an incomplete measure of species diversity, generally biased by the inability to collect all species in an assemblage and by the fact that not all species are equally abundant (Chao, Gotelli, *et al.* 2014). Several solutions to these problems have been proposed and are discussed in **Box 3** (page 15).

Finally, **species diversity** is sometimes **too simplistic**. Indeed, measures of taxonomic diversity are based on the following assumptions: (i) all species are equal, (ii) all individuals are equal (regardless of their size), (iii) the number and abundance of species have been correctly assessed with appropriate tools and in similar units (Magurran 2004). However, none of these assumptions are valid because (i) species are not equal in their effects on ecosystem functioning as their traits influence ecosystem processes; (ii) there is an inter-individual variation in how individuals of the same species use resources (e.g., for generalist species: an individual may overexploit one of the multiple resources known for the species); (iii) their number and abundance are generally very under-sampled, and almost impossible to sample reliably. Specific diversity is therefore not very representative of diversity, which is expressed in particular through the fact that the models testing the factors at the origin of species diversity patterns do not make it possible to distinguish between the various processes (e.g., disturbance, dispersion, environmental and spatial gradients, Chase *et al.*, 2005).

The trait-based approach

Functional diversity (i.e. the functional component of diversity) can be defined as "the value and range of traits of species and organisms that influence ecosystem functioning" (Tilman 2001). Measuring functional diversity means measuring the diversity of functional traits. Traits are, according to Kattge *et al.* (2011) "morphological, anatomical, biochemical, physiological or phenological characteristics measurable at the individual level (Violle *et al.* 2007) that reflect the result of evolutionary processes and community assembly responding to abiotic and biotic environmental constraints (Valladares *et al.* 2007)".

The functional approach has only recently been incorporated in animal ecology and for terrestrial arthropods (Pey *et al.* 2014, Moretti *et al.* 2017, Brousseau *et al.* 2018, Perović *et al.* 2018, Lowe *et al.* 2020). Although the term 'functional diversity' is widely used and accepted, we prefer to use the terms 'trait diversity' and 'trait-based approach' unless the functionality of traits has been assessed (by evaluating the relationships between traits and fitness along environmental gradients, see Wong, Guénard, & Lewis, 2019). However, for the majority of terrestrial arthropods, trait functionality has not been explicitly tested (Wong *et al.* 2019).

By considering traits, not species identity, it is possible to describe diversity patterns in a complementary way by considering the niche occupied by individuals. The niche can be defined as the set of environmental conditions, i.e., physical (e.g., habitat, temperature, humidity, pH) and resources (e.g., food, food size), in which stable populations can be maintained. Individuals and species co-existing in a community are then expected to share a set of traits selected by the environmental conditions. By taking into account the information carried by traits it is possible to obtain a better understanding of the **ecological processes** (deterministic vs. neutral) that determine the diversity of communities under different environmental conditions (McGill *et al.* 2006, Petchey & Gaston 2006, Mouchet *et al.* 2010, Webb *et al.* 2010, Leroy *et al.* 2014, Wong *et al.* 2019). While traits are measured directly on individuals, the trait approach allows for both inter- and intraspecific variation (Wong *et al.* 2019), valuable information for comparative studies in community ecology (Bolnick *et al.* 2011, Violle *et al.* 2012, Fontana *et al.* 2016).

Traits are also studied in reconstructions of ancestral morphologies (Harmon *et al.* 2010) or to understand how different traits have evolved between different phylogenetic clades (Kuntner & Coddington 2020).

The phylogenetic approach

Phylogeny is concerned with determining the **evolutionary history and relationships** of organisms. Relationships are assumed by phylogenetic inference methods that evaluate observed heritable traits (e.g., DNA, morphological traits) according to a specific evolutionary model. Evolutionary history and relationships between organisms are the results of selection pressures due to ecological and evolutionary processes (Mouquet *et al.* 2012) such as environmental sorting, competitive exclusion, immigration, and speciation (Gillespie 2004, Emerson & Gillespie 2008, Cavender-Bares *et al.* 2009). Thus, taking phylogenetic information into account informs us about the processes that determine diversity patterns, whether at the lineage or community level.

More recently, phylogenetic information has been used to calculate phylogenetic diversity indices (see Tucker *et al.* 2017 for a recent review) and better understand community diversity. Phylogenetic diversity is calculated from the branch lengths of a phylogenetic tree, separating species in a community. This approach is based on the assumption that the branching pattern of a phylogenetic tree reflects the accumulation of phenotypic, genetic, and behavioral differences between the evolutionary lineages. And that these accumulated differences can describe, explain or predict the evolutionary and ecological processes that drive community assembly (Tucker *et al.* 2017).

Phylogenetic diversity was considered for a time as a proxy for functional diversity (Prinzing *et al.* 2001, Webb *et al.* 2002, Cavender-Bares *et al.* 2009). It has since been shown that phylogenetic information is not a proxy for trait information (notably due to evolutionary

convergence¹ and phylogenetic niche² conservatism) and that it is complementary for our understanding of diversity and community assembly rules (Cadotte *et al.* 2013, Pavoine *et al.* 2013, Gerhold *et al.* 2015, Hacala *et al.* 2021, Ridel *et al.* 2021).

Combining the study of the main components of diversity

Diversities in taxonomic units, traits, and evolutionary units are linked. Organisms interact based on these traits, which determines the patterns of species coexistence (Tilman *et al.* 2014). Traits in turn are determined by the evolutionary origins of organisms and the environment in which they evolve.

Pavoine & Bonsall (2011) showed that comparing phylogenetic diversity with species (or taxon) diversity can reveal historical processes, including recent adaptive radiation, high rates of immigration, differences in speciation rates, and range expansion between lineages. They also showed that the combination of phylogenetic diversity and trait diversity can be used to disentangle assumptions about historical and biogeographic versus ecological processes in determining the species compositions of communities and regions. Thus, combining the phylogenetic approach with taxonomic diversity and trait diversity analyses allows for a better description of diversity patterns and the processes behind them. This unified approach (**Figure 2**) is promising and has been proven on many groups such as plants (Pavoine *et al.* 2011, Zhang *et al.* 2020), zooplankton (Gianuca *et al.* 2017), butterflies (Pavoine *et al.* 2014), or shrimps (Head *et al.* 2018).

To be able to combine these three components of diversity, it is necessary to have reliable knowledge of taxonomy, traits (and their functionality), and the phylogeny of the group studied. This is achieved by describing taxa, studying traits, and constructing phylogenies. However, for some groups of interest such as tropical terrestrial arthropods, we do not have access to this basic knowledge (Fichaux *et al.* 2019) and it is necessary to devote research effort to it (e.g., species description, trait measurements on individuals, determination of phylogenies). Once this information is acquired, reliable and comparable measures of the diversity of each of these components are needed.

¹ Evolutionary convergence is the result of evolutionary mechanisms that have led species, subject to the same environmental constraints (similar ecological niches), to independently adopt several similar physiological, morphological or behavioural traits (e.g., appearance of fins in fish, aquatic mammals and seabirds [morphologically winged, functionally finned]).

² Phylogenetic niche conservatism refers to the tendency of lineages to retain their ecological niche and associated ecological traits over time and through evolution.

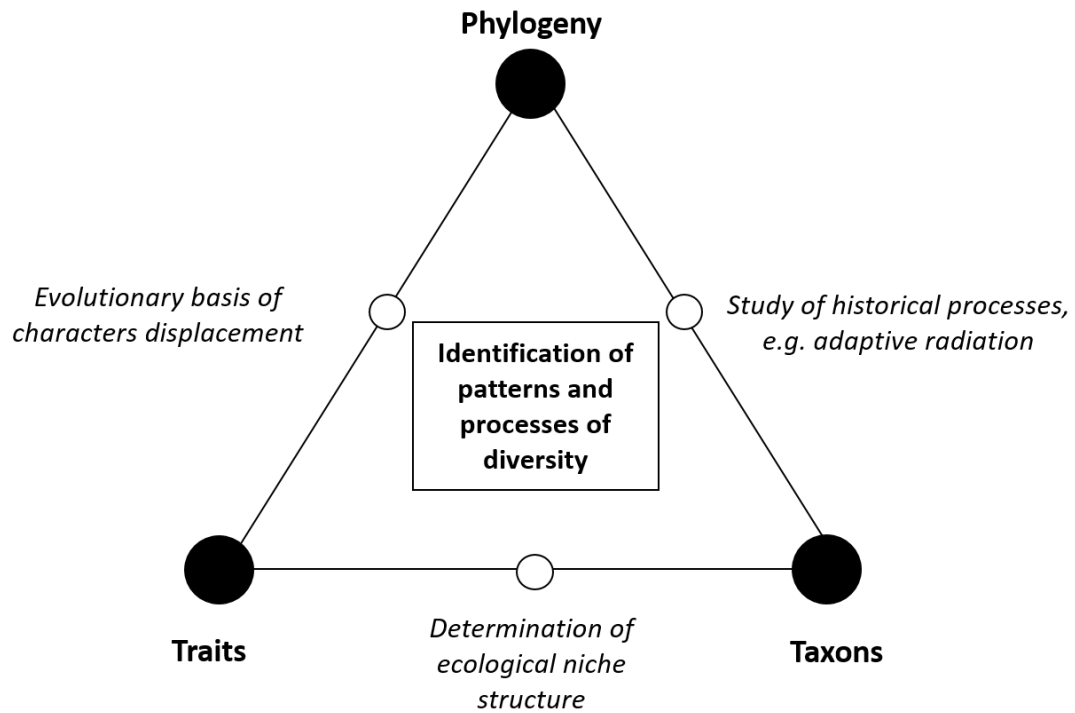


Figure 2: Diagram summarizing the contributions of the combination of taxa, traits, and phylogenies in identifying patterns and understanding the processes behind diversity. By studying patterns of phylogenetic diversity we can take into account historical and evolutionary processes in the assembly of communities. Studying patterns of taxonomic and trait diversity at the same time allows us to determine the structure of the ecological niche. Taking phylogeny into account in trait studies allows the evolutionary basis of the character shift that gave rise to the observed traits to be taken into account. Inspired by a diagram from Webb et al. 2002 on approaches integrating phylogeny, traits, and communities.

Box 3. Measuring diversity

Observed diversity patterns, and thus inferences about the processes behind them, depends on survey and sampling methods. In this section, we present the key parameters and steps for measuring diversity and describing its patterns reliably and as accurately as possible: sampling and measuring diversity.

Diversity sampling – The first step to accurate diversity determination is a standardized sampling of target organisms. Standardized sampling allows for a more reliable comparison of assemblages, and is preferred to ad-hoc sampling, although the latter may be locally more effective (Cardoso *et al.* 2009). Malumbres-Olarte *et al.* (2017) define standardized sampling as a compromise of seven criteria: (1) efficiency (yield), which depends on the sampling intensity, (2) suitability to the taxon and/or question asked, which depends in particular on the methods employed, (3) comparability between sites, habitats or biomes for example, even if the protocol is suboptimal for each site, (4) feasibility (given resources), (5) flexibility, (6) transparency (to be reproducible) and (7) reliability. The use of such protocols is particularly important for studies on hyperdiverse groups of organisms such as terrestrial arthropods. Yet, standardized protocols have been relatively rarely used and little comparable data exist on their diversity (Cardoso, Erwin, *et al.* 2011) (see the section on **Challenges in studying tropical spider diversity**, page 22 and following).

Diversity measures – Except for very well-known groups of organisms in very well-known locations, sampling is generally biased by undetected organisms (Coddington *et al.* 2009). Most assemblages contain rare species and assemblage sizes vary between habitats (Chao & Jost 2012, Chao, Gotelli, *et al.* 2014). Therefore, even if assemblages are sampled in a standardized manner, with sufficient sampling intensity, the samples are often incomplete and diversity is underestimated. To make standardized comparisons of diversity between assemblages, it is then necessary to use methods to estimate diversity (Gotelli & Colwell 2001, Chao, Gotelli, *et al.* 2014) and compare it at the same level of sampling completeness (Jost 2010, Chao & Jost 2012, Chao, Gotelli, *et al.* 2014). Historically, comparisons of estimated diversity have been made at the same sample size. However, the sample size does not take into account the fact that some assemblages are richer than others and therefore leads to an underestimation of large assemblages (Chao & Jost 2012). Sampling completeness represents the proportion of assemblage species represented in a sample (Chao & Jost 2012). Comparing estimated assemblage diversity based on completeness recognizes that more diverse assemblages require greater sampling effort to be properly characterized (see Roswell, Dushoff, & Winfree, 2021 for a review).

On the other hand, there is a myriad of possible measures of diversity, which do not all take into account the same information. Three broad categories of information carried by these indices have been identified: richness, evenness, and divergence (Magurran 2004, Moullot *et al.* 2005, Ricotta 2007, Pavoine & Bonsall 2011, Chao, Chiu, *et al.* 2014). **Richness** refers to the number of diversity units, be they species (or taxa), traits, or evolutionary units. **Evenness** (or Regularity) takes into account the distribution of abundances between diversity units and determines whether they are distributed equitably (Moullot *et al.* 2005). **Divergence** corresponds to a measure of dissimilarity between organisms, calculated from taxonomic, trait, or phylogenetic distances. The different existing indices vary in their consideration of these three types of information and can lead to different observations of assemblage diversity (Liu *et al.* 2007). The use of a single measure of diversity is therefore insufficient to provide a good representation of diversity and it is preferable to use a set of diversity indices together (Liu *et al.* 2007). **Unified measures of the three categories of diversity information** (richness, evenness, and divergence), as well as the three components of diversity (taxonomic, traits, evolutionary units), therefore provide a more complete picture of diversity (Pavoine & Bonsall, 2011; see in particular the use of Hill numbers by Chao *et al.*, 2014a, 2014b).

Spiders as a model for studying diversity

Spiders (Araneae) have been identified as a model group to study diversity patterns and the processes behind them (Cardoso, Pekár, *et al.* 2011, Birkhofer & Wolters 2012, Malumbres-Olarte *et al.* 2018). Yet, knowledge about their diversities remains poor. In this section, we summarize the aspects of spider diversity important for this thesis.

The evolutionary and ecological success of spiders

Spiders are considered by many researchers as a successful group (e.g., Bond & Opell, 1998; Blackledge, Coddington, & Gillespie, 2003; Kuntner & Agnarsson, 2011; Dimitrov & Hormiga, 2021). Some speak of ecological success, others of evolutionary success, without really defining them (but see Dimitrov & Hormiga, 2021).

Biological success is a concept dating from the mid-19th century that has most often been discussed in terms of comparisons between groups of organisms, at taxonomic or non-taxonomic levels, but always at a higher level than species (Wasik & Turner 2013). We have identified five consistent features in the literature in the notion of biological success: (1) diversity, (2) long evolutionary history, (3) the presence of key taxon-specific innovations (which we will group under the term evolutionary successes) as well as (4) ecological ubiquity and (5) abundance (which we will group under the term ecological success). Spiders meet all five of these characteristics:

- (1) Spiders are among the **most diverse terrestrial arthropods** (Wheeler *et al.* 2017) with over 49 900 described species (World Spider Catalog 2021). The total diversity of spiders is estimated to be between 76 000 and 170 000 species (Coddington & Levi 1991, Platnick & Raven 2013). Among chelicerates, spiders stand out for their extreme diversity (**Figure 3**). For example, they have 74 times more described species than their sister clade, the Pedipalpi.
- (2) Spiders are an **ancient taxon** with a long history of diversification beyond extinction. Their roots are estimated to be 400 million years old (Middle Devonian, Coddington & Levi, 1991; Fernández *et al.*, 2018). The ancestors of arachnids (a group including spiders, scorpions, ticks, Opiliones, etc., see **Figure 3**) probably lived in aquatic environments (Roy *et al.* 2015) (see **Figure 3** Pycnogonids, which are an aquatic group). Therefore, spiders may have been among the first animals to live on earth (Selden & Penney 2010), more than 150 million years before the dinosaurs.

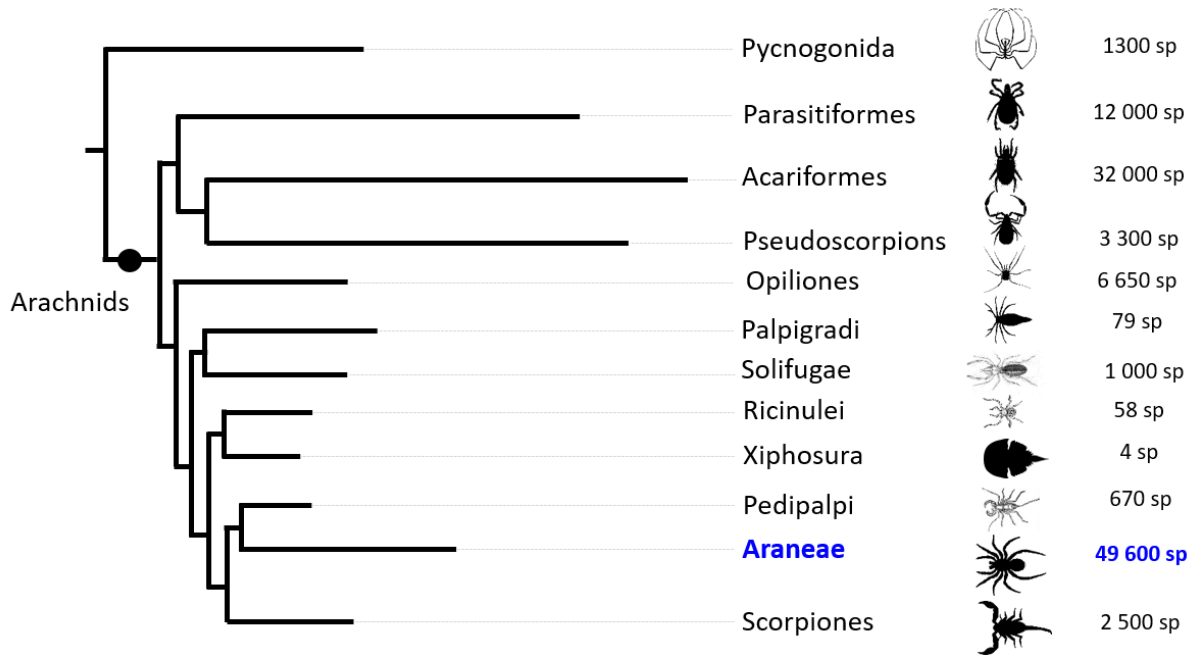


Figure 3: Representative diagram of the Chelicerates tree and their diversity, produced by taking the topology of the Chelicerates tree from Ballesteros et al. (2019). Branch lengths are not to scale.

- (3) Spiders exhibit a set of **key innovations** specific to their group such as their spinnerets (silk-producing organs), their tracheal respiratory system, their sensory system (hairs and slits distributed over a large part of their body), their various uses of silk, including different types of webs, their ability to produce venom, as well as their different hunting behaviors (see Dimitrov and Hormiga, 2021 for a detailed review).
- (4) The **ecology** of spiders is remarkable for their distribution, habitat affinity, and predatory role. Indeed, spiders are **distributed over the entire planet**, except in Antarctica (Natural Environmental Research Council 2012). Spiders are found in **all terrestrial ecosystems** (Turnbull 1973), from Arctic islands to desert regions, in areas of rich vegetation but also in poor environments such as caves, intertidal areas, and the tops of mountains and volcanoes (Foelix 2010). Despite their wide distribution, spiders often have very **specific habitat affinities** (Foelix 2010) and live in well-defined environments. The boundaries of these environments are determined by abiotic factors (temperature, humidity, vegetation structure) and biotic factors (available resources, competitors, enemies). As a result, spider species generally range following vegetation strata (Foelix 2010). In all these habitats, spiders are **the main group of predators** (Pekár *et al.* 2017). Indeed, spiders are all exclusively predatory (Meehan *et al.* 2009, Nyffeler & Birkhofer 2017) and mainly generalists (Pekár *et al.* 2012, Pekár & Toft 2015). In contrast to other hyperdiverse arthropod groups (e.g., Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera, and Acarinae), the evolutionary diversification of spiders is not the result of diet diversification (Rainford & Mayhew 2015). They do, however, exhibit a wide range of feeding strategies.

- (5) Spiders are **one of the most abundant groups** (Turnbull 1973, Coddington & Levi 1991, Nyffeler & Birkhofer 2017). Their density has been estimated at an average of 131 spiders per square meter over different areas of the globe (Turnbull 1973), and up to 1000 spiders per square meter under favorable conditions (Ellenberg *et al.* 1986).

Spider taxonomy

With 49,600 described species out of 76,000 to 170,000 potential spider species (Coddington & Levi 1991, Platnick & Raven 2013, World Spider Catalog 2021), not even half of the species are known. However, spider taxonomy (species discovery and description) is a field that is considered active (Agnarsson *et al.* 2013) and seems to be resisting the 'taxonomic impediment' (Rodman & Cody 2003, Engel *et al.* 2021, Jäger *et al.* 2021), with for example a total of 500 new species described between 2003 and 2013 (Agnarsson *et al.* 2013). In particular, the arachnological community has addressed the tedious issue of synonymy (i.e. description under different names of the same species by different taxonomists, thus biasing diversity estimates) by placing the list and taxonomic decisions in the public domain on the World Spider Catalog website (World Spider Catalog 2021). As with other poorly known but extremely diverse groups, the main factor limiting the development of spider taxonomy is the number of arachnologists to discover and study them (Platnick 1991, Foord *et al.* 2011, Agnarsson *et al.* 2013). However, we cannot wait until all species are described to study patterns of taxonomic diversity. Therefore, parataxonomic approaches are used to study the diversity of assemblages whose spiders are not known (see the section Working with unknown species pages 21-22).

Status of the trait-based approach in spiders

Patterns of trait diversity in spiders have not been as widely studied as those of their taxonomic diversity (Gallé *et al.* 2017). Traits have long been used as the main criterion in spider phylogeny (Agnarsson *et al.* 2013). However, the study of relationships between traits and environmental gradients, to determine the processes responsible for assemblages, dates back only about 15 years (**Box 4**).

This approach is therefore relatively new in spiders and still lacks a common framework (e.g., common measures, see **Box 4**). The functionality of traits has not been tested in spiders (as in most terrestrial arthropods, Wong *et al.* 2019 but see Moya-Laraño *et al.* 2013). Thus, many traits are being studied (**Box 4**), although it is unclear how these relate to environmental variables. Within this multitude of traits, the most used are hunting guilds and body size (**Box 5**).

Box 4. The trait diversity approach in spider assemblage studies

As an exploratory exercise, we reviewed published studies on the trait diversity approach in spiders through a World of Science query with the words 'trait', 'spider*' and 'function*' in April 2019. We identified 83 studies published between 2008 and 2019 on trait diversity in the context of studying the processes behind spider assemblages.

59 different traits were used in these studies, which can be classified into 7 categories (**Figure 4**): behavioral traits, dietary traits, environmental properties, life-history traits, morphological traits, phenological traits, and physiological traits. Some traits fall into more than one category at the same time. The 10 most abundant traits are listed in **Table 1**. The main categories of traits used are behavioral and feeding traits, as well as morphological traits and among them the hunting guilds and body size traits, respectively (confirmed by Pekar et al. accepted: **Appendix 2**).

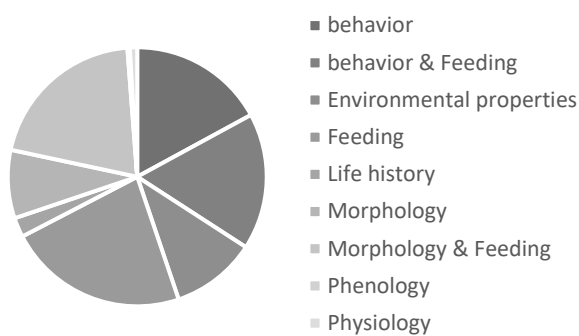


Figure 4: Categories of traits used in spider studies

Table 1: 10 main traits studied in spiders and their representativeness in the 83 studies reviewed.

Trait	Representativity
Body size	20%
Hunting guilds	18%
Dispersal ability	9%
Habitat preference	9%
Circadian activity	5%
Abiotic preference	4%
Diet specialization	4%
Phenology	2%
Leg size	2%
Eye size	1%

It is also noted that measurements of the same trait may vary between studies. For example, the body size trait can be the average total length of the spider (e.g., Ricotta *et al.*, 2011; Simons, Weisser, & Gossner, 2016; Schirmel *et al.*, 2016; Braaker *et al.*, 2017; Rigal *et al.*, 2018; Gallé *et al.*, 2018, 2019; Nagy *et al.*, 2018; Fernandez-Fournier *et al.*, 2018; Joseph *et al.*, 2018; Buchholz *et al.*, 2018; Turney & Buddle, 2019), only in females (e.g. Lambeets *et al.*, 2009; Gomes, Carvalho, & Gomes, 2018), total and opisthosoma length (e.g. Gibb *et al.*, 2015), prosoma length (e.g. Langlands *et al.*, 2011), prosoma length and width (e.g., Puzin *et al.* 2014, Lafage *et al.* 2015, Penell *et al.* 2018, Pétilion *et al.* 2018), the ratio between sternum width and length (e.g. Mammola *et al.*, 2018).

The large number of possible traits and measures suggests that there is no common approach or consensus on which traits should be used to resolve questions about the assembly of spider assemblages.

Of these 83 studies, more than half were interested in traits that they extracted from the literature (**Figure 5**). This highlights the most common practice in studies of trait diversity in spider assemblages, which is to retrieve trait values from the existing literature. Compiling trait values for species in the assemblages is then a laborious task because, for some traits and some species, the information does not exist or is not easily accessible because it is hidden in old publications or unpublished works (Moya-Laraño *et al.* 2013). This tendency to rely on traits from the literature reflects the fact that most of the studies were conducted in Europe (mainly Germany, France, Belgium, Czech Republic) (confirmed by Pekar et al. accepted: **Appendix 2**) in well-studied environments (forests and grasslands) for which information is more easily available from the literature.

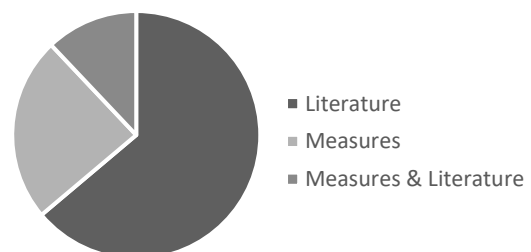


Figure 5: Sources of traits used in spider assemblage studies.

While the classification of hunting guilds has been proposed and reviewed several times (Uetz 1977, Uetz *et al.* 1999, Cardoso, Pekár, *et al.* 2011), no rules for measuring body size have been constructed for studies linking traits and environmental gradients (but see Jakob *et al.* (1996) for a measure in the context of fitness studies), so the different studies that address it use different measures (**Box 4**). Furthermore, the body size is a difficult trait to link to a particular filter as it is correlated with several types of factors (Brousseau *et al.* 2018) (e.g., metabolic (Brown *et al.* 2004 in Brousseau et Gillooly *et al.* 2001)), physiological (e.g., food deprivation, desiccation resistance), environmental (e.g., temperatures, resource use, vulnerability to natural enemies) (Cushman *et al.* 1993, Entling *et al.* 2010). Finally, the trait-based approach as it has been used over the last 15 years relies mostly on traits from the literature (**Box 4**), which has the advantage of being more easily accessible than having to make a set of measurements on many individuals but is limited to the information in the literature and does not take into account intra-specific variability.

Box 5. Spider hunting guilds

Spider guilds grouping species that similarly use the same resources (e.g., prey, habitats) (Blondel 2003), and thus reflecting their ecological niche, have been determined. Although many classifications of guilds exist, the main one used is the one based on feeding strategies (Cardoso, Pekár, *et al.* 2011), also called hunting guilds.

Hunting guilds are defined at the family level, assuming that they are conserved at the family level (Cardoso, Pekár, *et al.* 2011). Hunting guilds are generally classified into eight categories (Uetz *et al.* 1999, Dias *et al.* 2009, Cardoso, Pekár, *et al.* 2011) ranging from different web construction techniques - (1) sensing web weavers, (2) sheet web weavers (3) space web weavers and (4) orb-web weavers - to spider hunting techniques - (5) ambush hunters, (6) ground hunters and (7) other hunters - to (8) specialists. As members of the same guild may have similar functional roles in communities, spider hunting guilds were considered functional groups.

The conservatism of the family-level hunting guild has been questioned (Dias *et al.* 2009, Suter & Benson 2014) and some classifications take into account that different feeding strategies may be used within the same spider family (e.g., Dias *et al.* 2009).

The trait-based approach in spiders took a new turn at a workshop held in Christchurch, New Zealand, in 2019 entitled "Spider trait network: opportunities for a global collaboration to address broad-scale ecological and evolutionary questions". This workshop identified the challenges of creating a dedicated spider trait database, summarized by Lowe *et al.* (2020) (Appendix 1), and initiated its creation. Lowe *et al.* (2020) recall the need to create a global database of spider traits to unify our data (i.e. use the same terminologies and measures) and to improve the efficiency and reproducibility of studies using traits. They lay the foundations for such a database by defining traits, their standardization, the types of data accepted, and the governance of such a database. The **World Spider Trait database** (Pekár, Černecká, *et al.* 2021, Pekár, Wolff, *et al.* 2021, Appendix 2) was created in 2021. This database contributes to the construction of a general framework for studying traits. In the coming years, it will make it possible to determine the functionality of traits and to answer many questions in macroecology, biogeography and evolution by studying patterns of functional diversity at large

spatial and temporal scales and the relationships between trait diversity and phylogenetic diversity. It will then be possible to determine at large scales the relative contribution of environmental filters, dispersal and competitive exclusion in structuring patterns of specific and trait diversity in spiders.

Spider phylogeny

The **phylogenetic tree of spiders is just beginning to become clearer** (see **Figure 6** for the currently accepted topography) thanks to work carried out in recent years (Dimitrov *et al.* 2011, Garrison *et al.* 2016, Wheeler *et al.* 2017, Fernández *et al.* 2018, Kulkarni *et al.* 2020, Kallal *et al.* 2021).

Research on spiders has been rather slow to incorporate molecular phylogeny approaches, starting with a few studies in the 1990s (e.g., Gillespie, Croom, & Palumbi, 1994; Gillespie, Croom, & Hasty, 1997; Zehethofer & Sturmbauer, 1998). Molecular phylogeny studies have proliferated since then, but our understanding of the spider tree and the fundamental relationships between families and species has been greatly slowed by the inadequacy of the molecular markers available to address these questions in spiders (e.g., 12S in Lycosidae (Vink *et al.* 2002), 18S (Kreherwinkel *et al.* 2018), 28S (Murphy *et al.* 2006)). The advent of Next Generation Sequencing (NGS) technologies and the development of phylogenomic and transcriptomic approaches have enabled the resolution of basic spider tree relationships (Agnarsson *et al.* 2013, Brewer *et al.* 2015, Garrison *et al.* 2016, Garb *et al.* 2018, Kallal *et al.* 2021).

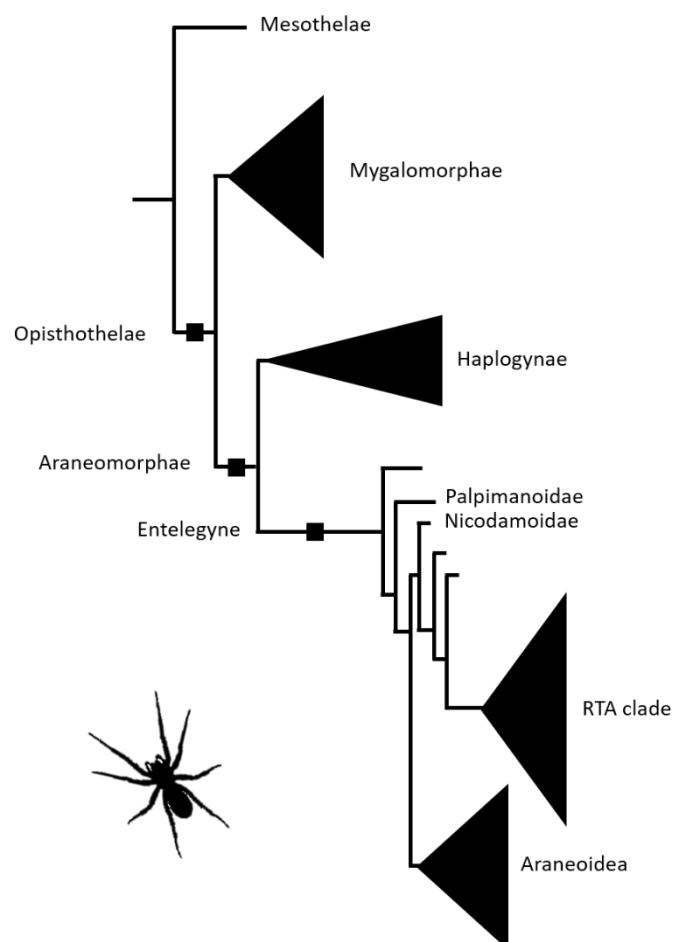


Figure 6: Diagram of the spider tree representing the major lineages identified to date. RTA stands for retrolateral apophysis. Simplified schematic version of the trees produced by Kulkarni *et al.* 2020. Branch lengths are not to scale.

However, **whole sections of the spider tree are still poorly studied**. For example, the relationships between wolf spiders (family belonging to the RTA clade and one of the most diverse, World Spider Catalog, 2021) are still poorly understood (but see Piacentini & Ramírez,

2019). The wolf spider family has therefore been highlighted as one of the priorities for future phylogenetic research on spiders worldwide (Garb *et al.* 2018).

As a result, few studies have focused on phylogenetic diversity (confirmed by DNA) to determine the diversity patterns of spider assemblages and the processes behind them (Ulrich *et al.* 2010, Cardoso 2012, Dolson *et al.* 2020, Hacala *et al.* 2021, Ridel *et al.* 2021). Due to the lack of knowledge on spider phylogeny, these studies have determined phylogenetic diversity based on taxonomic classification, assuming that taxonomic classification reflects phylogenetic relationships (Ulrich *et al.* 2010, Cardoso 2012), or by combining phylogenetic trees with taxonomic classification (Gonçalves-Souza *et al.* 2015, Hacala *et al.* 2021, Ridel *et al.* 2021).

Known diversity patterns and processes in spiders

Diversity is very unevenly distributed within the main lineages of spiders (see lineages in **Figure 6**). For example, there are about 3,000 species in the Mygalomorph lineage, compared to over 46,000 in the Araneomorph lineage, which is over 90% of all known species. The Araneomorphs, therefore, contain more than 15 times as many species as their sister group of the same geological age, the Mygalomorphs. This imbalance has led to the formulation of several hypotheses on **the processes responsible for the diversification of spiders**, reviewed by Dimitrov & Hormiga (2021). Through a synthesis of recent work, these authors (1) show that the importance of the factors traditionally considered as the main responsible for spider diversification is less: co-diversification with insects, the role of silk, web architecture, and food web loss; and (2) suggest that less explored factors such as environmental heterogeneity, sexual selection, genome architecture or the microbiome may have played an important role in the diversification of spiders. Studies of spider radiations highlight that **diversification patterns vary greatly between lineages** (Gillespie 2016) with some lineages characterized by weak ecological differentiation, and others by strong ecological differentiation. For example, in the Hawaiian Archipelago, *Tetragnatha* (Tetragnathidae) and *Ariamnes* (Theridiidae) show repeated episodes of ecological differentiation (Gillespie 1991, 2013, Blackledge *et al.* 2003, Blackledge & Gillespie 2004, Gillespie & Rivera 2007, Gillespie *et al.* 2018). In contrast, *Orsonwelles* (Linyphiidae) all have similar ecologies (Hormiga *et al.* 2003).

As with most terrestrial organisms, **a latitudinal gradient of species diversity** is found in spiders with the most diverse assemblages found in **tropical ecosystems** (Santos *et al.* 2017, Piel 2018). However, this pattern is not found for trait diversity, with Cardoso *et al.* (2011b) showing that trait richness was not always higher in tropical regions compared to temperate regions. Studies of spider diversity patterns at large scales are, however, limited by the mere availability of coarse data at these scales due to the lack of knowledge on spider diversity (Dimitrov & Hormiga 2021).

Thus, most research on spider diversity patterns consists of local and regional scale studies of alpha and beta species diversity (e.g., Yanoviak, Kragh, & Nadkarni, 2003; Entling *et al.*, 2007; Hore & Uniyal, 2008; Baldissera, Rodrigues, & Hartz, 2012; Barton *et al.*, 2017). These studies show **relationships between spider species richness and environmental variables**, with, for example, a higher number of species in more structurally complex habitats (Greenstone 1984, Yanoviak *et al.* 2003, Entling *et al.* 2007, Baldissera *et al.* 2012, Ávila *et al.* 2017), a different diversity between micro-habitats (e.g., Whitehouse *et al.*, 2002; Barton *et al.*, 2017) and vegetation (e.g., Hore & Uniyal, 2008). Studies taking traits into account show that trait diversity of spiders is influenced by habitat type and structure (e.g., Schirmel, Blindow, & Buchholz, 2012; Corcuera *et al.*, 2016). The few available studies on the phylogenetic diversity of spiders (Ulrich *et al.* 2010, Cardoso 2012, Cardoso *et al.* 2014, Dolson *et al.* 2020, Hacala *et al.* 2021, Ridel *et al.* 2021, Steinke *et al.* 2021) have also shown that the diversity of their assemblages is constrained by environmental filters. Moreover, within terrestrial arthropods, spider assemblages appear to be more structured by environmental variables and less by competition than those of other taxa dominating the terrestrial soil macro-arthropofauna such as carabids or ants (Wise 2006, Fichaux *et al.* 2019, Hacala *et al.* 2021).

Environmental variables related to habitat thus seem to have **an important role in structuring the diversity of spider assemblages**.

Study of the diversity of spiders in tropical environments

Hotspots of diversity

Tropical environments are the most species-rich terrestrial ecosystems and among the least well-known (Gentry 1992). Characterizing and understanding the factors that drive tropical diversity has inspired generations of ecologists, leading to fundamental advances in theoretical and evolutionary ecology (Chazdon & Whitmore 2002). Yet these studies have focused on vertebrates and plants, neglecting most invertebrate taxa, even though they represent the majority of eukaryotic diversity in these environments (May 2011). Tropical forests are notably the richest environments for terrestrial arthropods (Miller *et al.* 2002) with 1.5 million described species and over 10 million estimated species (Hamilton *et al.* 2010). And among tropical arthropods, spiders are one of the most diverse taxa with at least several hundred species per hectare of forest and an estimated diversity of at least a thousand species per forest (Agnarsson *et al.* 2013). Yet we still know little about the species diversity of tropical spider assemblages at local (between habitats) and regional scales, and consequently about the factors that determine this diversity. This lack of knowledge is linked to the extreme diversity of tropical environments, which makes it more difficult to study the patterns and processes behind it.

The difficulties of studying the diversity of tropical spiders

Characterizing and understanding hyperdiverse assemblages such as those of tropical spiders is an overwhelming but necessary task. All the more necessary in the current context of global warming and habitat loss due to deforestation that is hitting tropical ecosystems hard (Malhi *et al.* 2008), which are seeing their diversity disappear before it can even be described. Arachnologists have been trying to describe this diversity for more than thirty years (e.g., Coddington *et al.*, 1991) and have accumulated methodological difficulties linked to the extreme diversity of assemblages and the lack of knowledge about them (Coddington *et al.* 2009).

The results of studies conducted in recent years on the standardization of sampling methods (Sørensen *et al.* 2002, Coddington *et al.* 2009, Malumbres-Olarte *et al.* 2017) and analysis methods (Chao & Jost 2012, Chao, Gotelli, *et al.* 2014) have produced a set of recommendations for the study of hyperdiverse assemblages.

Rethinking sampling for the tropics

Sampling in tropical environments requires a **rethinking of the sampling strategies and methods used due to the extreme species diversity of the assemblages**. Acquiring accurate and comparable data on hyperdiverse assemblages requires the **application of reliable, efficient, and standardized sampling protocols**.

- (i) Unfortunately, protocols that follow such criteria remain rare and it is not clear that they can be applied to hyperdiverse arthropod communities in tropical environments (Malumbres-Olarte *et al.* 2017). It is, therefore, necessary to **develop standardized protocols specifically adapted to tropical environments**.
- (ii) On the other hand, studies testing the suitability of commonly used protocols and methods on spider species assemblages worldwide have shown that even intensive sampling in tropical environments is negatively biased by under-sampling (Novotný & Basset 2000, Sørensen *et al.* 2002, Coddington *et al.* 2009, Agnarsson *et al.* 2013), which results in a high propensity of singletons (represented by a single individual), and causes an underestimation of the true richness of assemblages. Also, the **sampling intensity** required to get a reliable idea of species richness in tropical environments is much higher than that known in temperate environments.
- (iii) Finally, the known vertical gradient of temperate vegetation is not found in the tropics (Basset *et al.* 2003) and the stratification of the arthropofauna in the vegetation does not seem to follow the same laws as in temperate regions (Basset *et al.* 1992, 2003). The **sampling methods** used are therefore not likely to be equally effective. It is, therefore, necessary to question and test the relevance of these methods in the context of sampling hyperdiverse assemblages in tropical forests.

Taking undersampling into account

Statistical methods used to determine the patterns and drivers of diversity in hyperdiverse assemblages must **take into account their undersampling**. Since the more individuals sampled, the more species found (Gotelli & Colwell 2001), and the more rare species found, sample richness may not stabilize as sample size increases in a realistic sampling scheme (Coddington *et al.* 2009, Chao, Gotelli, *et al.* 2014). It is, therefore, necessary to use **diversity estimators that take into account the completeness** (or coverage) of the sampling (Jost 2010, Chao & Jost 2012), i.e. the proportion of species that were sampled.

Working with unknown species

Finally, the third difficulty in obtaining accurate and comparable data on tropical spider species assemblages is that these spiders are not known.

In general, spiders are a taxon for which identification to species is complex and requires expert taxonomic knowledge. However, the number of experts is too small to describe all species. In the context of tropical spider assemblages, the majority of species are therefore undescribed (Robinson *et al.* 2009, Cardoso, Pekár, *et al.* 2011) and assemblages are extremely diverse (Agnarsson *et al.* 2013). Coddington *et al.* (2009) estimate that spider diversity in undisturbed tropical rainforests is rarely less than several hundred species per hectare. However, taxonomic resources are not sufficient to delimit and describe species at the same time as studying assemblages (Agnarsson *et al.* 2013). It is therefore necessary to use para-taxonomic approaches by identifying individuals at the morpho-species level (Oliver & Beattie

1993, 1996a, b): taxa are identified, separable based on obvious morphological differences, without a priori knowledge. In some cases, however, e.g., wolf spiders (Lycosidae), the morphospecies approach is not sufficient because morphological conservatism is such that we lack informative characters to define and separate species and even genera (Vink *et al.* 2002). Consequently, their diversity can only be studied by molecular approaches.

As tropical spiders are relatively undescribed, the only possibility to study their trait diversity is to measure them (Schuldt *et al.* 2014, Liu *et al.* 2015, Schuldt & Staab 2015, Pétilion *et al.* 2018). The classification of hunting guilds has been adapted to spiders in Neotropical environments (Höfer & Brescovit 2001, Dias *et al.* 2009). This shows that in the Neotropical spiders there is variation in hunting guilds within the same spider family between genera (**Box 5**), e.g., in the Lycosidae there are sight-hunting spiders, web-weaving spiders, and sedentary burrowing spiders. Furthermore, knowledge of the natural history and ecology of Neotropical spiders is so incomplete that this classification will need to be revised as more knowledge about these spiders accumulates (Höfer & Brescovit 2001, Dias *et al.* 2009).

As the majority of tropical spiders have not been described by science, each new sample necessarily contains species observed for the first time (Agnarsson *et al.* 2013). Thus, there is a need to study the phylogenies of these spiders to describe their diversity patterns and integrate them into assemblage-scale studies.

To our knowledge, there is no study to date that addresses the three components of diversity (taxa, traits, and evolutionary units) in tropical spider assemblages.

OBJECTIVES AND THESIS ORGANIZATION

This thesis falls within the general framework of describing diversity patterns and characterizing the ecological processes that determine them at the scale of assemblages. This question has a long history in ecology but has not been answered globally because patterns of diversity and the processes at their origin vary between groups of organisms and, for the same group, between ecosystems. Spiders, as an abundant and diverse group with high ecological importance, are a model group in ecology whose study should allow a better understanding of the processes responsible for diversity patterns. Their diversity patterns seem to be determined mainly by deterministic ecological processes linked to their environment and applied at local scales. Tropical environments, because of their very high diversity of spiders and habitats, are environments that allow us to test the ecological processes responsible for diversity patterns. To date, however, these advances are severely limited by the almost total lack of knowledge about spider diversity in these ecosystems.

In this context, the question of this thesis is the following: **what are the patterns of diversity and the processes responsible for it in spiders in tropical environments?**

The originality of this thesis is to use taxonomic (**Part I and II**), trait (**Part II**), and phylogenetic (**Part III**) approaches to describe spider diversity patterns at mainly local scales in different tropical habitats.

Characterizing the diversity patterns of tropical spiders requires the development of reliable sampling protocols and the comparison of sampling methods (**Chapter 1 and 2**). As knowledge of spider taxonomy and traits is lacking, it is necessary to use para-taxonomic approaches (**Chapters 1, 2, 3, and 4**), phylogenetic approaches (**Chapter 5**), and testing of different traits (**Chapter 4**) to describe diversity patterns. Comparative studies of diversity patterns in different habitats (**Chapters 1, 2, 4, and 5**) and between biomes (**Chapter 3**) then allow hypotheses to be made about the factors structuring diversity. Overall, these complementary approaches provide a more complete picture of the diversity patterns of spiders in tropical environments.

In **Part I** of this thesis we were interested in determining the taxa diversity of spider assemblages from different Neotropical habitats and studying the factors structuring it by applying standardized protocols, testing sampling methods, using the morpho-species approach, and standardizing statistical analyses using richness estimators.

- In the **first chapter** (Privet *et al.* 2020), we focused on spider assemblages in the soil stratum, comparing the effectiveness of two commonly used sampling methods for this stratum in describing diversity patterns of spider assemblages along the habitat complexity gradient.

- In the **second chapter** (Privet *et al.* 2018), we developed and tested a quasi-optimal sampling protocol (i.e., optimized for several sites) to characterize the diversity of soil and vegetation spiders and to study variations in assemblage diversity between two tropical forest habitat types.

In **Part II** of this thesis, we explored the contribution of taking into account trait diversity to describe and understand the diversity patterns of spider assemblages in different Neotropical habitats.

- In the **third chapter** (Privet & Pétilion 2020), we compared patterns of taxonomic and trait diversity between tropical and temperate ecosystems.
- In the **fourth chapter** (Privet *et al.* in prep.), we tested different traits and compared taxonomic and trait diversity of contrasted tropical forest habitats to infer the factors driving the assemblages.

In **Part III**, we used the phylogenetic tool to determine the diversity patterns of a spider family in a tropical archipelago with very diverse ecological conditions and to highlight the role of different habitats in its evolutionary radiation.

- In the **fifth chapter** (Privet *al.* in prep), we determined the patterns of phylogenetic relationships between spiders living in different habitats and made inferences about the origin of their radiation.

In the **General Discussion**, we discuss all these results and open up perspectives for next research on tropical spider diversity patterns and processes.

In the appendix, the work I have been involved in alongside this thesis is presented. **Appendix 1** (Lowe, [...], Privet, *et al.* 2020) promotes the creation of an open global spider trait database and lays the groundwork for it. **Appendix 2** (Pekàr, [...], Privet, *et al.* 2021) presents the World Spider Trait Database. **Appendix 3** (Courtial, Privet, Picard & Pétilion, submitted) presents a species description of tropical forest jumping spiders (Salticidae) using an integrative taxonomy approach. **Appendix 4** (Pétilion, Privet, *et al.*, 2020) presents a study of spider assemblages in Hawaiian forest fragments and the increasing occurrence of exogenous species in these assemblages.

PART I: FACTORS STRUCTURING TAXONOMIC DIVERSITY OF TROPICAL SPIDERS

METHODOLOGICAL STANDARDIZATION AND ASSESSMENT OF ECOLOGICAL FACTORS INFLUENCING TAXONOMIC DIVERSITY OF SPIDERS BETWEEN TROPICAL HABITATS

CHAPTER.1

Efficiency of Pitfall Trapping vs. Nocturnal Hand Collecting in Assessing Soil-Dwelling Spider Diversity along A Structural Gradient of Neotropical Habitats

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Abstract

Assessing spider diversity remains a great challenge, especially in tropical habitats where dozens of species can locally co-occur. Pitfall trapping is one of the most widely used techniques to collect spiders, but it suffers from several biases, and its accuracy likely varies with habitat complexity. In this study, we compared the efficiency of passive pitfall trapping versus active nocturnal hand collecting (NHC) to capture low understory-dwelling spider taxonomical (morphospecies) and functional (hunting guilds) diversity along a structural gradient of habitats in French Guiana. We focused on four habitats describing a structural gradient: garden to the orchard to the forest edge to the undisturbed forest. Overall, estimated morpho-species richness and composition did not vary consistently between habitats, but abundances of ground-hunting spiders decreased significantly with increasing habitat complexity. We found habitat-dependence differences in taxonomic diversity between sampling strategies: NHC revealed higher diversity in the orchard, whereas pitfalls resulted in higher diversity in the forest. Species turnover resulted in high dissimilarity in species composition between habitats using either method. This study shows how pitfall trapping is influenced by habitat structure, rendering this sampling method incomplete for complex, tropical environments. However, pitfall traps remain a valuable component of inventories because they sample distinct assemblage of spiders.

Keywords: Araneae; Guiana shield; sampling methods; diversity indices; functional diversity; species richness; turnover.

Introduction

Spiders constitute a mega-diverse taxon, with more than 48,000 species described to date [1] and still many new species found every year. To get reliable estimates of local spider diversity, ecologists and conservationists need a robust sampling protocol, i.e., standardized (repeatable in space and time, without introducing bias), and optimized (with a maximized ratio of sampling effort by collected diversity) for realistic sampling given time and resource constraints [2–4]. To achieve such a standardized and optimized sampling protocol, the selection of cost-effective complementary methods is a critical issue [5]. Previous work on sampling protocol optimization was mainly conducted in Mediterranean and temperate systems (see [3,4]), but few studies have compared methods in highly diverse systems such as tropical forests [6,7]. Yet, it remains unclear which sampling protocol would provide reliable estimates of spider diversity in tropical systems. Because spiders have developed a wide range of hunting strategies (e.g., ambushing, wandering, web building, door trapping) and inhabit varied habitats and vegetation strata (from the ground to canopy), several sampling methods need to be integrated to get a reliable description of the whole assemblage. Nevertheless, the number of collecting methods should be limited to minimize the complexity of a sampling protocol and to maximize its repeatability. The objective of this study is, therefore, to evaluate the robustness of sampling methods in tropical forests. In that respect, we focused on tropical low understory-dwelling spiders because there is less consensus to sample this stratum in forests despite its lower spider diversity compared to other strata [6,7].

Previous studies on low understory-dwelling spiders showed that this stratum needs to be studied with special care in order to obtain representative estimates [8–10], especially because sampled diversity changes with the sampling method [11,12]. In tropical forests, however, there is no consistency between the methods used to sample low understory-dwelling spiders. For example, Vedel et al. [13] used hand collection and litter sifting, Malumbres-Olarte et al. [6] used hand collection, cryptic searching, and pitfall traps, and Privet et al. [7] used pitfall traps and litter sifting.

Pitfall trapping is the most widely used arthropod sampling technique to collect spiders worldwide [12,14–16]. This method was shown to be efficient in catching ground-dwelling spiders in a variety of ecosystems, including temperate forests [17], Mediterranean shrublands [3], agrosystems, and grasslands [11,18], and bare grounds [19]. However, pitfall traps appear to be less efficient in tropical forests [6,7,13], and they may suffer from several important biases, including the under-studied effect of habitat structure [20,21].

Together with litter sifting (specially designed for small and low mobile species: [7]), nocturnal hand collecting (NHC) is an alternative method to sample low understory-dwelling spiders. This method was found to be efficient by Azevedo et al. [5], in particular, as it shows no bias between day and night spider diversity sampling in tropical forests [7,22]. Yet, depending on the collectors' experience, NHC is cheap and requires less effort than pitfall traps [5,23].

Hence, it is still unclear whether pitfall trapping should be used to perform a standardized protocol, or whether nocturnal hand collecting should be included to develop an optimized protocol. Moreover, although the efficiency of pitfall trap sampling is likely to be influenced by habitat structure, as with other passive methods, no study to date has assessed how its efficiency could change along a structural gradient of habitat.

Here we compare the efficiency of two widely used sampling techniques, pitfall traps, and NHC, to capture **taxonomic** and **functional diversity** of low understory-dwelling spider assemblages along a broad gradient of tropical habitats in French Guiana. We hypothesize that the sampling efficiency of passive methods (i.e., pitfall traps) would decrease when habitat structural complexity increases [20]. In contrast, we predict little variation in sampling efficiency for the active method of NHC [21].

More precisely, we expect a difference in the estimated taxonomic diversity between methods to increase along the increasing gradient of habitat structural complexity (tested by comparing rarefaction curves between methods habitat by habitat). Second, we expect species composition of spider assemblages to differ between methods and vary more with habitat structure with pitfall traps than with NHC (tested by determining beta diversity between methods per habitat and beta diversity between habitats per method). Finally, we hypothesize that hunting guilds diversity (a proxy of the functional diversity assessed by guilds composition and relative abundances per method per habitat) would be more affected by changes in habitat structural complexity with pitfall traps than with NHC.





Materials and methods

Site

To compare the efficiency of low understory-dwelling spider sampling methods along a structural gradient of Neotropical habitats, we focused on four different land-use types along the road Degrad Saramaka, near Kourou, in French Guiana. The habitats sampled were: (i) home garden, (ii) small orchard after slash and burn, (iii) forest edge, and (iv) undisturbed tropical forest (see Table 1 for GPS [global positioning system] coordinates, pictures, and Corine Land Cover codes). The garden habitat had the least vegetation cover with mainly short-cut grass, some herbaceous patches, a few ornamental flower bushes (*Ixora* sp. [species]), and some young trees such as mango trees. The orchard habitat was a lowland rain forest cut out and planted with tree species producing fruits (mango, banana, lemon, orange, cashew nut, coconut, and other palm trees), a variety of bushes (pineapple, spinach, and manioc), and some herbaceous cover. The forest edge was adjacent to a road and an open area such as gardens. It was 50 meters deep into the vegetation, so its aspect was similar to forest areas. The forest was a primary lowland tropical rain forest area with the typical vegetation of seasonally flooded forest of coastal French Guiana. We established one plot of 50m x 50m in each of the four land-use types, and inside an area of 20 km² (Table 1) to limit changes in soil type and hydrological characteristics. The local climate is typically equatorial

with a fairly constant temperature across the year (around 26.1 °C with 1.3 °C difference between the lowest and the highest temperature for 2001–2012) with high humidity divided into two main seasons: heavy rainfall between December and August and dry with few rains between September and November, giving an average annual precipitation about 283 cm per year [24].

Table 1. Coordinates and Corine Land Cover Classes of the four habitats along the habitat complexity gradient.

				
	Garden	Orchard	Edge	Forest
GPS coordinates	5°04'43.3"N 52°40'36.8"W	5°04'58.6"N 52°41'47.3"W	5°04'15.0"N 52°41'33.8"W	5°04'11.4"N 52°41'48.1"W
Corine Land Cover 2012 code and libellee	2430 – Land principally occupied by agriculture, with significant areas of natural vegetation	3111 – Broad-leaved forest	3111 – Broad-leaved forest	3111 – Broad-leaved forest

Sampling protocol

In order to sample ground-dwelling spiders, we used circular pitfall traps and NHC. Following the COBRA protocol [4,15], we set up 25 pitfall traps (eight centimeters in diameter) in a grid of 5 m × 5 m in each plot (five lines of five pitfalls spaced by 10 m across each 250 m² plot). The pitfall traps were filled one-third full by ethylene glycol for killing and preserving specimens fallen in the traps. The pitfall traps remained active for 15 days. In each plot, this method required a team of two people working two hours to install 25 pitfall traps and one hour to collect samples, resulting in a total effort of six person-hours per plot. While the pitfall traps were active, we sampled spiders using NHC along the lines traced by pitfalls. This method required two experienced persons sampling low understory with a headlamp for half an hour during night-time in each plot looking for moving spiders and eyeshine. This gave a sampling effort of one person-hour per plot for NHC. Sampling was conducted from the 15th to the 29th of July 2013, corresponding to the end of the raining season in French Guiana. The climate in July 2013 in Kourou oscillated between 28 to 33 °C, with an average of 4.46 mm of precipitation per day [25].

Taxonomy

Individuals were sorted and identified at the species level, defining morpho-species when there were no matching species in the literature [13,26–28]. Spider samples, separated by morpho-species from each sampling technique, were stored in 70% ethanol. When juvenile spiders were old and characteristic enough to be identified at the species level, we included

them. All spiders are deposited within the reference collections of the UMR EcoFoG, Kourou (French Guiana).

Hunting guilds

Trait functions have not been explicitly tested for spiders, especially in tropical habitats, and using traits when there is no evidence for their functionality runs the risk of attributing patterns in community functional structure to false mechanisms [29]. Here we assessed functional diversity by assigning hunting guilds to genera and families. We are aware that guilds describe more a group of species than a functional attribute per se [30] and that guild classification at the family or genus level does not integrate inter- nor intraspecific variability [31], which are important in structuring assemblages. We followed the hunting guilds classification described in Cardoso et al. [31], except for Trechaleidae placed in specialists by Cardoso et al. [31] and described as hunters by Dias et al. [32]. The guilds were the following: (1) sensing, (2) sheet, (3) space, (4) orb-web weavers; (5) specialists; (6) ambush, (7) ground, and (8) other hunters.

Data analysis

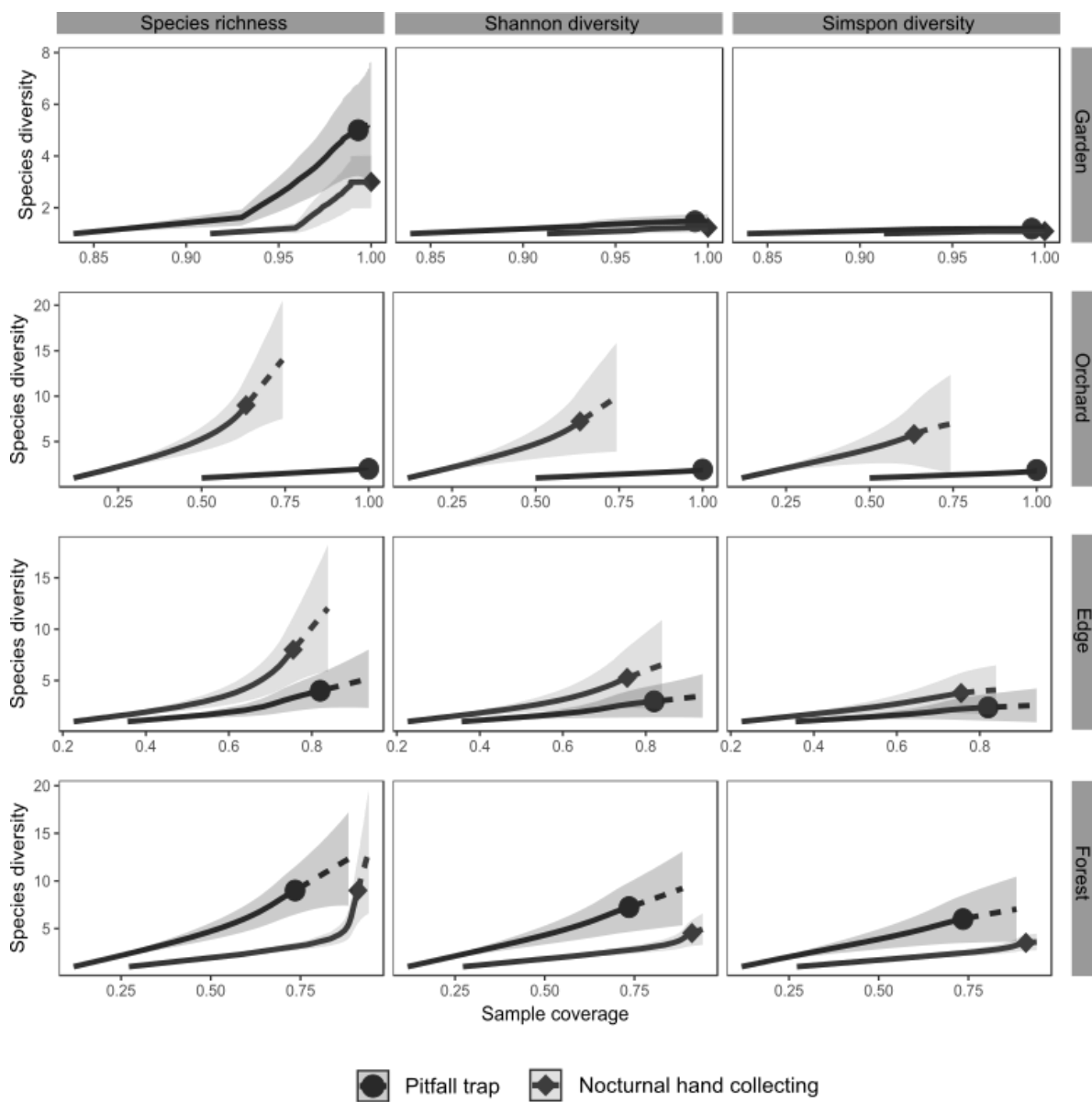
The 25 pitfall traps per habitat were pooled to make pitfall samples comparable to one hour NHC per habitat (following [6] methods and results). Taxonomic diversity per sampling method was assessed using rarefaction and extrapolation curves based on sample coverage [33,34]. We characterized the taxonomic alpha diversity of spider communities using complementary species and abundance-based indices: (i) taxonomic richness, (ii) Shannon, and (iii) Simpson diversities [33]. Analyses were completed using the R-based iNEXT package [33,35]. Extrapolations were realized using the asymptotic Chao1 estimator [36]. 95% confidence intervals (CI) were calculated, and non-overlapping of CI indicates a difference at a level of 5 percent between expected diversities [33]. Changes in species composition (taxonomic beta diversity) (i) between methods within a habitat and (ii) between habitats per method were assessed by computing pair-wise dissimilarities on abundance data using the Bray indices family and separating the turnover and nestedness-resultant components of taxonomic beta diversity using the betapart R package [37,38]. Guilds composition and relative abundances were compared between methods and habitats (i.e., pitfall garden vs. NHC garden; pitfall orchard vs. NHC orchard, etc.). Changes in guild composition were tested by statistically comparing the relative abundance of the dominant guilds among habitats using χ^2 tests. All analyses were conducted using the R software version 3.4.3 [39].

Results

We sampled a total of 355 spiders (213 adults and 142 juveniles) representing 18 families and 40 morpho-species (see Table S1 for composition). Similar total numbers of individuals were collected by both methods, 174 by pitfall traps and 181 by NHC.

Among the 18 morpho-species that were not singletons, four (22%) were collected by both methods. The NHC technique collected specimens belonging to 28 morpho-species from 11 families and representing seven hunting guilds (ground, other and ambush hunters, sheet, orb, sensing web weavers and specialists). Pitfall traps sampled spiders from 18 morpho-species from 11 families representing four hunting guilds (ground hunters, other hunters, sensing web weavers, and specialists).

Patterns of taxonomic alpha diversity were consistent between diversity metrics (i.e., species richness, Shannon and Simpson indices); taxonomic alpha diversity was significantly higher in the orchard but lower in the forest when using hand-collection compared to a pitfall, and it showed no differences between the methods in the garden and edge (Figure 1). Yet, taxonomic alpha diversity did not consistently vary with habitat complexity.



Species composition collected by the two methods was almost completely dissimilar. This dissimilarity was mainly due to species turnover in all habitats, except in gardens where assemblage composition was much more similar between methods. In this case, the few differences were linked to assemblage nestedness (Table 2). Assemblages were almost completely dissimilar among habitats for both methods, and this dissimilarity was mostly due to species turnover (Table 3).

Table 2. Species composition dissimilarity and its decomposition by habitat between pitfall traps vs. nocturnal hand collecting (β : beta diversity = total dissimilarity between pitfall and NHC; β_{TURN} : partition of the beta diversity linked to turnover; β_{NEST} : partition of the beta diversity linked to nestedness).

	Garden	Orchard	Edge	Forest
β	0.22	1	0.93	0.81
β_{TURN}	0.05	1	0.9	0.61
β_{NEST}	0.17	0	0.03	0.20

Table 3. Decomposition of beta diversity among habitats and by sampling methods (β : beta diversity; β_{TURN} : partition of the beta diversity linked to turnover; β_{NEST} : partition of the beta diversity linked to nestedness).

	Garden			Orchard			Edge		
<i>Pitfall</i>	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}
Orchard	1	1	0						
Edge	0.97	0.8	0.17	1	1	0			
Forest	1	1	0	1	1	0	0.93	0.9	0.3
<i>NHC</i>	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}
Orchard	0.9	0.68	0.22						
Edge	1	1	0	1	1	0			
Forest	1	1	0	1	1	0	0.89	0.8	0.09

Figure 1: Estimated taxonomic diversity (species richness, Shannon and Simpson diversities) in all 4 habitats for each sampling method. 95% confidence intervals are represented in light color and were obtained by 200 bootstrap replications. Plain lines represent interpolated diversity whereas dotted lines extrapolated.

Guild composition significantly changed among habitats for both methods when considering pitfall traps and NHC separately (χ^2 tests, 6df, $\chi^2 = 403.97$, and $\chi^2 = 274.29$, $p < 0.001$, respectively) with a replacement of ground hunters by other hunters and web builders. On the other hand, patterns of guild relative abundance differed between methods only for the orchard and forests (Figure 2).

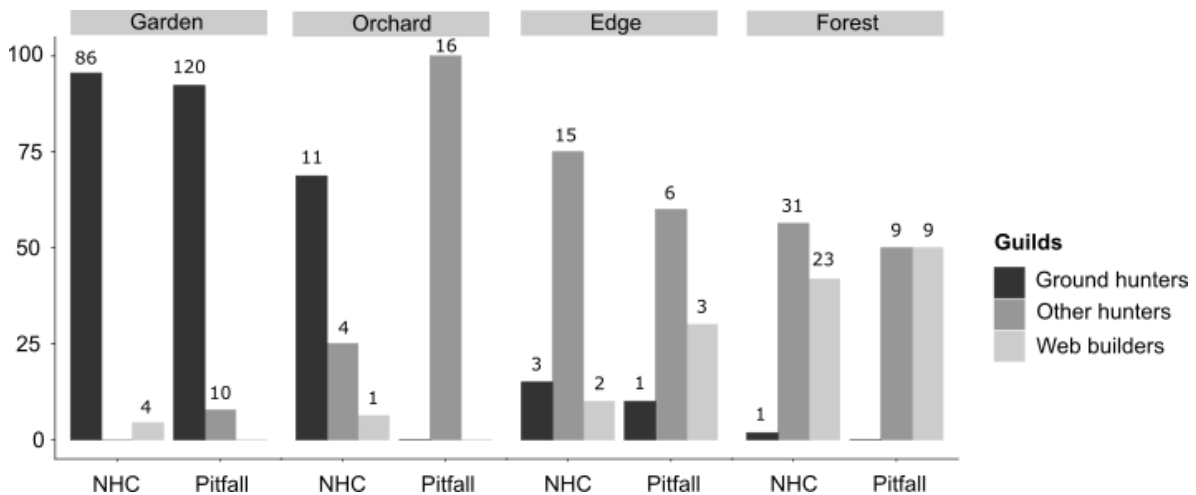


Figure 2: Relative abundance in hunting guilds along the structural gradient of habitats collected by Nocturnal Hand Collecting (NHC) and pitfall traps. For simplification purpose, we grouped guilds as follows: (1) ground hunters: ‘ground hunters’, (2) other hunters regroups the ‘other hunters’, ‘ambush hunters’ and ‘specialists’ guilds, and (3) web builders: ‘sensing web weavers’, ‘sheet web weavers’, ‘space web weavers and ‘orb web weavers’. Absolute numbers are presented above each bar.

Discussion

In this study, we compared for the first time the efficiency of the two most common sampling methods to collect tropical soil-dwelling spiders, namely pitfall traps and Nocturnal Hand Collecting (NHC), across contrasting habitats in French Guiana. Our results showed that the difference between the two methods in capturing soil-dwelling spider taxonomical diversity varies according to the sampled habitat, though not consistently. Although we performed intensive sampling, the number of individuals was low, and the proportion of singletons was high, which is typical of tropical forests where many species are locally rare [40].

Differences in taxonomic alpha diversity between pitfall trapping and NHC did not significantly increase along the structural gradient of habitats. Contrary to our expectation that the difference of estimated taxonomic diversity between passive and active methods increases along the increasing gradient of habitat structural complexity, we actually found that taxonomic alpha diversities differed between methods only in orchard and forest. Our results in garden and forest edge are in line with two previous studies performed in the Mediterranean and temperate ecosystems [5,15] that found pitfall traps and NHC to be both efficient methods to collect soil-dwelling spiders.

However, NHC was more efficient than pitfall traps to collect spider taxonomic alpha diversity in the orchard, which may be due to the fact that pitfall traps would capture only species that actively hunt, while NHC would allow sampling species with a wider variety of hunting strategies (such as traps, silk nets or ambushing). Indeed, this was confirmed by our

finding that NHC captures a more functional diversity of spiders than pitfall traps in this habitat. This result is in line with those of Sereda et al. [41], who found that hand-collection was better than pitfall traps for capturing ground-dwelling spider diversity in a temperate forest. Conversely, NHC was less efficient than pitfall traps to collect spider taxonomic richness in tropical rainforests. NHC efficiency relies on the sight of the person who samples, which would be reduced by the complexity and heterogeneity of the tropical rainforest habitat. The experience of collectors can also play an important role, which was not the case here because all collectors were experienced. Previous studies found that pitfall traps were unsuitable in estimating the diversity of ground-dwelling predators like spiders in tropical rainforests and other temperate woody habitats [5–7,20,42]. Here we showed that neither pitfall traps nor NHC alone is sufficient for sampling the whole taxonomic alpha diversity of ground-dwelling spiders in Neotropical forests. Even if we choose to compare one-hour NHC (2 people, ½ hour per person) with the pool of 25 pitfall traps left 15 days on the field (versus five pitfall traps left for 5–8 days in [6]), we still observed that pitfall traps and NHC result in a similar number of sampled individuals. Comparing taxonomic alpha diversity relatively to sample completeness, our results suggest that an increase in sampling effort with NHC will not allow its efficiency to surpass those of pitfall traps. Further methodological investigations comparing other sampling methods such as litter sifting [7] or hand collection in quadrats [23] are thus needed to get a proper estimation of the diversity of ground-dwelling spiders in tropical rainforests.

In addition, the taxonomic composition of spider assemblages was almost completely different when sampled by pitfall traps and NHC, and this dissimilarity was linked to species turnover except in the garden habitat. Contrary to our expectation, the difference in taxonomic composition between methods did not increase along the increasing gradient of structural habitat complexity. Moreover, taxonomic beta diversity was not more affected by changes in habitat complexity with pitfall traps. As NHC and pitfall traps do not sample the same species, both methods should be used concomitantly when aiming at inventorying spiders in tropical habitats. The fact that turnover of spider assemblages was driven by species turnover rather than by nestedness has already been reported from a large variety of habitats, such as temperate wet meadows, ponds and grasslands [43–45], forests [46], grey dunes [47] or African mountains [48]. In the garden habitat, assemblages sampled by NHC and pitfall traps were less dissimilar, and this dissimilarity was mostly linked to species nestedness: there were species and abundance loss between the methods and no species replacement. Gardens are less complex, more open, and disturbed than other habitats. Its spider assemblage is very little diversified, as exemplified by the strong dominance of one single species (a Lycosidae). Consequently, pitfall traps and NHC sample nearly the same spider assemblage in this highly disturbed habitat, and may be interchangeable when sampling Neotropical garden, and other habitats with simple structure and low relative diversity. On the other hand, one should also consider that the small number of morpho-species common to both methods could be the result of the high proportion of singletons. As singleton proportion can be reduced by

increasing sampling effort (although most tropical species are considered few abundant), the composition distinctiveness of these two methods could also decrease.

One intriguing aspect of our results concerns the proportion of males and females caught during the sampling. Pitfall traps are known to catch mature males to a higher degree than other sampling methods, including NHC, due to the higher reproductive activity of males. Consequently, pitfall traps catch a larger percentage of identifiable spiders. If we confirm that pitfall traps caught more adult spiders, we, however, found that both methods catch more females than males. Considering spider functional beta diversity (assessed by hunting guilds), dissimilarities between methods did not increase along the increasing gradient of habitat complexity, contrary to our prediction. NHC sampled higher guild richness in all habitats, which suggests that NHC is more efficient than pitfall trapping for collecting the overall functional diversity of soil-dwelling spiders in Neotropical habitats. However, both NHC and pitfall traps showed the same gradual change of guild composition across habitats, with a shift from ground hunters dominated-assemblages in garden habitat to assemblage dominated by ‘other hunters’ in forests (i.e., other hunters and ambush hunters, sensu [31]). Hence, even if pitfall traps collect fewer guilds, they still capture important elements of functional diversity. These results are in line with those found along an urban-rural transect in temperate regions [49], although functional changes were not systematically reported [50,51].

Unlike studies performed on other biomes, we suggest an optimized protocol using NHC to collect soil-dwelling spiders rather than pitfall traps in relatively simple tropical habitats (i.e., gardens, orchards, and edges) for ecological studies because it collects higher taxonomic and guild diversity and requires up to six-fold lesser sampling effort than pitfall traps, while still capturing similar abundances of soil-dwelling spiders and guilds shift along the gradient. However, following Tourinho et al. [52], we suggest that NHC alone is not sufficient to provide a complete picture of spider assemblages in tropical habitats and should be used in association with beating tray methods. Besides, we showed that the efficiency of NHC is more limited than pitfall traps in complex habitats such as Neotropical forests, which contradicts previous results (e.g., [6]). Knowing that pitfall traps are less efficient than litter sifting in the tropical forest [7], we suggest combining NHC with litter sifting as based methods for ecological studies of ground-dwelling spiders in this habitat, complemented by beating methods as well. However, we recommend studies with inventory purposes to use a combination of these methods as NHC and pitfall traps sample different species assemblages.

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<i>Pisauridae</i> sp.1				1				
<i>Thaumasia</i> sp.13								22
Salticidae								
<i>Salticidae</i> sp.39	2							
Segestriidae								
<i>Segestriidae</i> sp.1		1						
Sicariidae								
<i>Sicariidae</i> sp.1				1				
Sparassidae								
<i>Sparassidae</i> sp.7				1				
Tetragnathidae								
<i>Leucage</i> sp.2						1		
Trechaleidae								
<i>Trechalea</i> sp.1								1
<i>Trechalea</i> sp.8						1		
<i>Trechaleidae</i> sp.9								1
<i>Trechaleidae</i> sp.6							1	
TOTAL	130	90	16	16	10	20	18	55

CHAPTER.2

Spider assemblage structure in a Neotropical rainforest-inselberg complex: ecological and methodological insights from a small-scale intensive survey

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[**Erratum**]: during the writing of this thesis we detected some missing sentences to the published version of this article that we added.

Abstract

Despite the huge diversity tropical arthropods represent, factors shaping their communities are still poorly known, especially at small spatial scales. In this study, we aimed at providing ecological and methodological insights from a short and intensive field sampling of spiders, a highly diverse group of predators. We investigated how sampling methods, habitat type and day-time affect diversity and composition of spider assemblages. The standardized sampling protocol was applied in a tropical rainforest in French Guiana, where both ground- and vegetation-dwelling (up to 2.5 meters) assemblages were sampled during day and night using supposedly complementary methods at low and high (granitic hills called inselbergs) elevations. Observed and estimated richness of vegetation-dwelling spiders, as well as their species composition, did not differ between methods (sweep netting vs. beating). Observed species richness was much lower in pitfall traps than in litter samples, which suggests a low mobility of ground-dwelling spiders and reveals the inadequacy of the former method compared to the latter. Spider assemblage in the vegetation of inselberg was two times poorer than in lowland forests and dominated by different families, probably due to harsher habitat conditions there. Strongly different patterns were here highlighted between vegetation and ground-dwelling spider assemblages, the latter being less diversified than in the vegetation which deserves further attention.

Key words: Araneae, composition, day-time, French Guiana, non-parametric estimators, richness, sampling method.

Introduction

Assessing spatial patterns in organisms' diversity, and understanding their ecological determinants, is still one of the most fundamental topics in modern ecology. Yet our knowledge derives primarily of vertebrates and plants studies; much less is known about the structure of terrestrial arthropod communities despite they represent the most diversified taxa with highest species richness. Arthropods are especially speciose in tropical rainforests where nearly 1.5 million species have been currently described out of an estimated number of 3 to 11 million tropical rainforests could host (Hamilton *et al.* 2010, 2013).

Among terrestrial arthropods, spiders are one of the most diversified groups of arthropod predators worldwide (Nentwig 2013), with high bio-indicative values (e.g., Marc *et al.* 1999). Indeed, spiders are abundant occupying a wide range of spatial niches (Kremen *et al.* 1993) and inhabit almost every terrestrial habitat. Numerous studies have investigated the driving factors of spider assemblages in temperate habitats, such as vegetation structure, or habitat management (e.g., Hatley & Macmahon 1980; Lafage *et al.* 2015; Prieto-Benitez & Mendez 2011; Scharff *et al.* 2003). However, we still know much less regarding the factors that drive spider assemblages in tropical forests, where most of the studies have been carried out with inventory objectives or at the population level (Azevedo *et al.* 2014; Coddington *et al.* 1991; Dias *et al.* 2009; Scharff *et al.* 2003; Sereda *et al.* 2014; Sørensen *et al.* 2002). This is particularly true in French Guiana where spider assemblages have been the subject of several inventory surveys (see Vedel & Lalagüe, 2013; Vedel *et al.* 2015) and where a list of spiders have been recently updated (Vedel *et al.* 2013) but where the determinants of assemblages are still misunderstood. Tropical rainforests of the Guiana Shield are characterised by the existence of different and contrasting forest habitats. They differ in their ground texture and fertility, their seasonal water stress and the associated forest structure (Baraloto *et al.* 2011). These habitats included “terra firme” to seasonally flooded lowland rainforest and sometimes rocky outcrops named inselbergs, which rise abruptly from the surrounding landscape. Lowland rain-forests lie in low-lying areas near rivers where episodic flooding often submerges ground surfaces during periods of high precipitation (Baraloto *et al.* 2007). On the opposite, inselbergs exhibit very particular ground and microclimate conditions: alternation of heavy rain and severe drought with air temperature and insolation that regularly reach values that are considerably higher than average values in surrounding forests (Kounda-Kiki *et al.* 2004). Then, inselbergs are considered as “xeric island” or “microclimatic desert” (Porembski 2007). Vegetation of inselbergs is starting to be known, and studies highlighted that these habitats host a characteristic vegetation mosaic (Porembski 2007; Sarthou *et al.* 2003, 2010). In contrast, little research has been devoted to the fauna of inselbergs ecosystems, especially for invertebrates (Kounda-Kiki *et al.* 2004; Lees *et al.* 2014; Sarthou *et al.* 2009; Vedel & Lalagüe 2013) and spiders (Vedel *et al.* 2013). Inselbergs are considered less rich than surrounding rainforest, but to date, no direct study has compared their assemblage to that of other forest habitats.

Even in well-studied tropical habitats, spider assemblages, as for arthropods in general, are larger than measured due to high frequencies of rare species (in average 32% of singletons;

Coddington et al. 2009) whatever the sampling effort. Tropical forest sampling of spiders is then a difficult task with the need of using a combination of different sampling methods (e.g., Cardoso et al. 2009; Jiménez-Valverde & Lobo 2005) and a high sampling effort to collect a significant part of the fauna (Coddington et al. 2009). Thus, it has been underlined that to get significant knowledge on the ecology of particular indicator taxa, quasi-optimal design (sensu Malumbres-Olarte et al. 2017) using complementary sampling methods is still needed. Moreover, comparisons based on observed species numbers are misleading and could have important implications in answering ecological questions. In addition, day vs. night period sampling seems to be an important factor influencing the composition of spider assemblages (Cardoso et al. 2009; Coddington et al. 1991; Sørensen et al. 2002) and could potentially explain part of singletons due to nocturnality (Coddington et al. 2009). In fact, spiders are known to be mostly active only at night and a smaller proportion is active only during the day (Foelix 2010).

In this study, we applied an intensive quasi-optimal protocol by day and night on vegetation- and ground-dwelling spider assemblages from inselberg and lowland rainforests at the Nouragues National Nature Reserve in French Guiana. We focused on species richness and assemblage composition as the main response variables (e.g., Azevedo et al. 2014; Coddington et al. 1996; Lafage & Pétilion 2016; Prieto-Benitez & Mendez 2011) with the aim of investigating the effect of habitat type on diversity and composition of spider assemblages

We focused on spider assemblages of the two more accessible strata: understory vegetation and ground leaf litter. In understory stratum, the two sampling methods known to be the most efficient are the sweep net and beating tray. These methods target different microhabitats with sweep net targeting lower understory vegetation and the beating tray higher understory vegetation (Coddington et al. 1991; Vedel & Lalagüe 2013). Regarding the ground stratum, pitfall traps remain one of the most widely used methods for studying ground-dwelling macro-arthropods in general (Spence & Niemelä 1994) and especially spiders, while depletion quadrat with litter sifting, despite being time-consuming, also seems to represent an interesting complementary method (e.g., Baars 1979; Mantzouki et al. 2012). As we used two different and supposedly complementary methods on each stratum, during two periods of the day, we also aim at bringing some new method-logical insights on spider sampling in tropical rain forests, particularly in inselberg forests.

More specifically, we tested the following hypotheses. (i) Microhabitat influences the diversity of vegetation-dwelling spider assemblages. We thus expect species richness and composition to be different between both sampling methods targeting understory vegetation. Moreover, these two sampling methods sampled different volumes of habitat (i.e. sweeping sampled twice the volume of habitat of beating). Thus, we expected spider species richness to follow changes in the volume of habitat sampled by the different methods. (ii) Pitfall trap sampling can be considered as a surrogate of other, time-consuming, sampling methods like litter sifting (e.g., Baars 1979; Mantzouki et al. 2012) for ground-dwelling spiders. Thus we expected species richness, abundances (caught by pitfall traps) and densities (caught

by litter sifting) to be correlated, whereas composition was expected to differ slightly between methods, with more mobile species caught by pitfall traps. (iii) Diversity of spider assemblage changes along with the type of tropical forest habitat. We expected vegetation and ground-dwelling spider assemblages' species richness to be less rich in inselberg forests compared to lowland forests due to harsh climate conditions and less depth of ground layer found on inselbergs (Kounda-Kiki et al. 2004). In the same way, we expected the species composition of spider assemblages to be significantly different between inselberg and the nearby lowland forests, as it has been found for vegetation (Porembski 2007; Sarthou et al. 2010). (iv) Daytime influences the activity of vegetation and ground-dwelling spiders. Thus, night assemblages were expected to be richer than day ones (Foelix 2010) and to have different species compositions (Cardoso et al. 2011).

Materials and methods

Study site

The fieldwork was carried out in the Nouragues national nature reserve (French Guiana; 4°04'18"N; 52°43'57"W). Sampling was done during nine consecutive days and nights early during the rainy season (6–15 December 2013), which is considered by Vedel & Lalagüe (2013) as the best sampling period. It was achieved in two rainforest habitats: (i) lowland seasonally flooded rainforest located in the Pararé area, and (ii) low forest located on the top of the Nouragues inselberg (411 m above sea level). Lowland vegetation is typical of primary lowland rainforest, with few inclusions of different vegetation types: palmito-swamp forests, liana forests and bamboo forests. Canopy height varies between 30 and 50 m. The Nouragues inselberg is a rocky outcrop isolated from the rest of the forest where the ground is washed away and the ground granitic. Hence, only a few but specialized species survive in this harsh environment (Porembski 2007). The low forest found nearby the top of this inselberg is rich in Myrtaceae with many endemic plants. It is characterized by a significant number of shrubby species or small bushy shrub with multiple stems and trees with leaning stems. Other trees have tapering trunk. Canopy height ranges from 8 to 15 m high.

Sampling design and field work

A standardized protocol was established to assess differences between lowland and inselberg habitats on spider rainforest assemblages inhabiting the ground and understorey vegetation, and to compare assemblages observed during day vs. night collecting for both strata. This protocol is described, tested and criticized for the first time in this study.

Two surface-standardized active sampling methods targeting understorey vegetation species were selected. First, sweep netting was carried out in the lower herb layer or shrubby vegetation with a sweep net along 20 m long and one meter wide (arm length plus sweep handle) transects, representing a sampling volume of 50 m³ each. Twelve stratified transects were conducted per period (day and night) by the same two persons.

The second method consisted of vegetation beating to collect spiders living in the shrub, high herb vegetation, bushes, and small trees. A stout stick was used to hit branches or other vegetation in order to collect falling specimens on a beating tray placed underneath. These samples were conducted in 9 × 9 m quadrats where the vegetation was beaten to a height of 2.5 m allowing to sample about 22.5 m³. Twelve stratified quadrats were conducted per period (day and night) by two duos concurrently (six quadrats per duo).

As in our protocol, sweep netting sampled twice the volume-habitat of beating, we investigate if species richness of assemblage collected followed the same pattern, i.e. being two times richer by sweep netting than by beating.

Two methods were used to sample ground-dwelling assemblages. First, pitfall traps constituted by circular, 10 cm diameters, plastic traps containing ethylene glycol as a preservative were used. Fifteen pitfalls have been arranged along a line, spaced 10 m apart (Topping & Sunderland 1992), and were set over a period of two days (days plus nights) in each habitat. They allow estimating the abundance of ground-dwelling spiders. The second method consisted in litter sifting conducted by using a Winkler extractor as a depletion method to estimate the density of spiders on 1 m² as in Groc et al. (2009), hereinafter called 'litter sifting'. Hand sorting of these samples was conducted in the lab. Fifteen 1 m² litter samples were spatially pair-matched with pitfall traps and conducted per day and per night (total thirty). Pitfall traps and litter samples were spatially paired to test if pitfall traps can be considered as a surrogate of litter sifting.

A total of 186 samples were collected from the Nouragues Nature Reserve, 96 from vegetation and 90 from the ground, with 93 samples from each habitat (see Table 1).

Table 1. Summary of spider sampling by each method, for both lowland and inselberg habitats. Nb.: number, ad.: adults, prop.: proportions.

	Inselberg				Lowland				Total
	Pitfall	Litter	Beat	Sweep	Pitfall	Litter	Beat	Sweep	
Nb. replicates	15	30	24	24	15	30	24	24	-
Nb. Individuals (ad.)	35 (21)	51 (15)	196 (66)	205 (64)	23 (4)	77 (20)	270 (101)	404 (109)	1261 (420)
Nb. morphospecies	12	14	44	38	4	17	66	80	216
Prop. singletons (%)	67	93	80	71	100	82	74	71	67
Prop. doubletons (%)	25	0	9	8	0	18	11	15	18

Sorting and identification

Samples were fixed and preserved in 70% ethanol. Individuals were first sorted and identified to family following Dippenaar-Schoeman & Jocqué (1997), Adis (2002), and Jocqué & Dippenaar-Schoeman (2006). Because of the lack of taxonomical knowledge about tropical spiders we defined morpho-species (MS) based on morphological traits, mainly by observation of genitalia and habitus. Under a 65 microscope, we realized a side-by-side comparison of specimens to determine distinct morphological entities. Both juveniles and adults were identified at the family level. Because only adults are identifiable at species level, no morpho-

species were defined based on juveniles. Juveniles were then excluded from the richness measures, although they represented ~60% of the specimens. When it was possible, sexes were matched based on color patterns and physical characteristics. For each identified morpho-species a unique code was assigned and a reference individual was designated to take images of dorsal and ventral body views and genitalia. All individuals are deposited at the University of Rennes 1 (Rennes, France).

Statistical analyses

Correlation between pitfall traps and litter sifting

To test if pitfall sampling can be considered a surrogate of litter sifting, we used correlation to compare pair-matched data using $\log(x+1)$ transformed data. Litter sifting, and especially pitfall trap, collected few adult spiders (Table 1). There was no significant difference between abundances (pitfall traps) and densities (litter sifting) (Generalized Linear Model, abundances ~ methods, $F_{1,0.2} = 1.57$, $P = 0.21$) and there were either not significantly correlated (Spearman correlation test, $r = -0.17$, $P = 0.38$, $n = 30$). Hence data from pitfall traps were omitted from subsequent analyses.

Influence of methods, habitat, daytime and strata on morphospecies richness

To test if habitat, daytime, methods and strata influence observed species richness, generalized linear models (GLM) were carried out. First, a model comprising all factors and their interaction was carried out. Type of error (Poisson vs. Quasi-Poisson) was selected by comparing residual deviance and denominator freedom degree (O'Hara & Kotze 2010). A second model was calculated if interaction was not significant. We estimated the expected species richness by using different non-parametric estimators: Abundance-based Coverage Estimator (ACE) (Chao & Yang 1993), Incidence-based Coverage Estimator (ICE) (Lee & Chao 1994), Chao1 and Chao2 (Chao 1984 1987), Jackknife 1 and Jackknife 2 (Burnham & Overton 1978, 1979), which determined the least number of species present in the assemblage (Mao & Colwell 2005). Such estimators do not show dependence to unequal sampling effort between modality (Basset et al. 2012) and they show little dependence to the number of rare species, however a minimum sampling effort is needed to produce a reliable estimation (Chao et al. 2009). Richness estimators were compared using species rarefaction curves (Gotelli & Colwell 2001). Sample coverage was calculated for each sample according to Chao & Jost (2012) method and sampling intensity was calculated as the ratio of adult number on species richness (Coddington et al. 1996).

Influence of methods, habitat and daytime on assemblage composition (morpho-species)

To test for differences in assemblage composition between methods (beating vs. sweeping and pitfall vs. sifting), habitat (inselberg vs. lowland forest) and daytime (day vs. night samples), we conducted an analysis of similarities using PERMANOVA (PERmutational

Multivariate ANalysis Of VAriance, 9999 permutations) on the corrected Bray-Curtis index (Clarke et al. 2006).

Analyses were made using R software (R Development Core Team 2013), except for richness estimators that were calculated with EstimateS software (Colwell 2013).

Results

A total of 1261 spiders were collected belonging to 35 families and 216 morpho-species. Among them, 1075 vegetation-dwelling spiders (17% adults) and 186 ground-dwelling spiders (32% adults) were collected with a high proportion of singletons (67%; Table 1). The intensity of this sampling was 1.9.

Influence of methods, habitat and daytime on species richness

Despite the difference in sampled habitat volume between both vegetation sampling methods, sampling intensity was nearly the same with 1.5 and 1.7 for beating and sweeping on the inselberg and 1.5 and 1.6 in lowland, respectively. Observed richness was not significantly different between methods used to sample vegetation-dwelling spiders (Table 2). Non-parametric richness estimators did not highlight high differences between beating and sweeping methods (Table 3). Estimators never stabilized with the increase of the number of individuals sampled as neither of the species rarefaction curves reached an asymptote (Fig. 1).

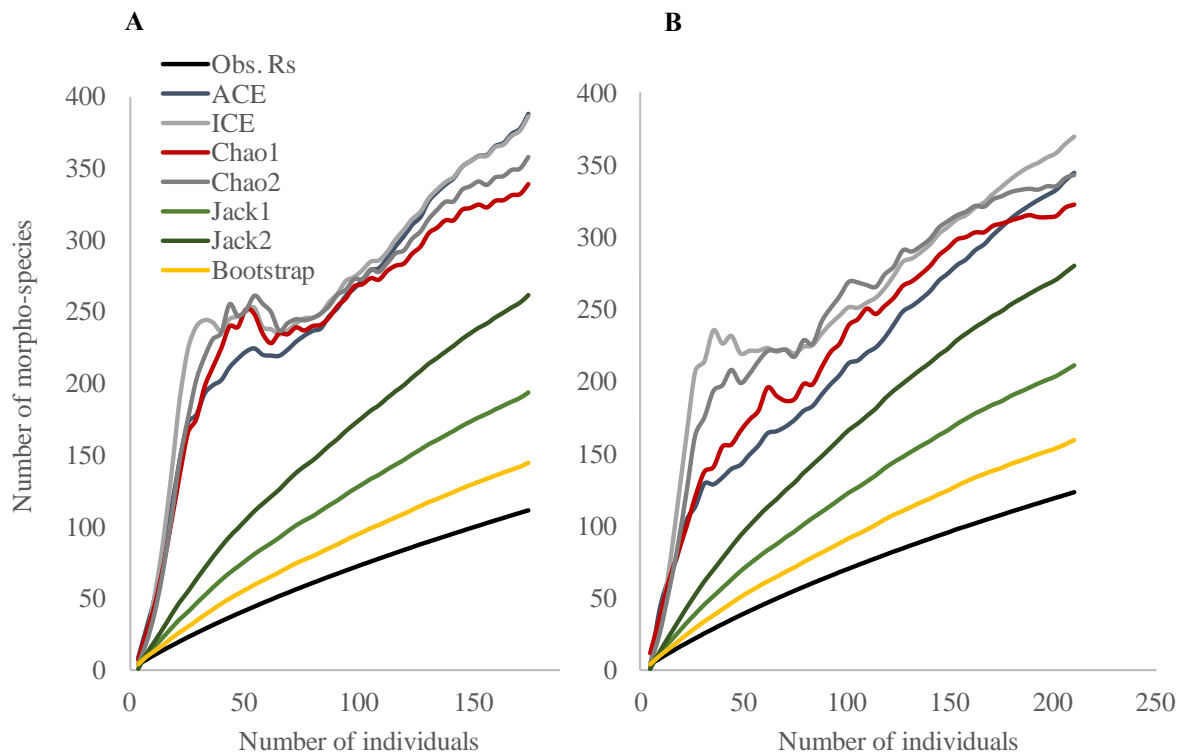
Observed species richness was significantly higher in lowland than in inselberg for vegetation-dwelling spiders (Table 1; Fig. 2), but not for ground-dwelling spiders collected by litter sifting where there was no difference of observed species richness between both habitats (Table 2). The different non-parametric richness estimators comparing habitats did not show an asymptote with the increase of sample set (Fig. 3). These curves showed that the expected richness was higher in lowland than in inselberg for both ground and vegetation assemblages. Moreover, the sample coverages were very small for all samples with 46% of the estimated fauna diversity sampled by beating, 58% by sweeping, 63% by pitfall trap and 14% by litter sifting on the inselberg, and 52%, 55%, 0% and 32%, respectively, in lowland rainforest. Comparisons of the estimated species richness (Table 3) show that the estimated species richness is higher in lowland compared to inselberg forests for vegetation-dwelling spiders, but it is higher in inselberg forests for ground-dwelling spiders.

There was no significant difference in species richness between day and night for both vegetation and ground-dwelling spider assemblages (Table 2).

The sampling intensity was nearly the same for both strata with an average of 1.12 for the ground and 1.54 for the vegetation. Vegetation-dwelling species richness was significantly higher than that of ground (Generalized Linear Model, richness \sim strata, $F_{1,36} = 160.76$, $P < 2.2e^{-16}$; Table 1), which was confirmed by the rarefaction curves showing that estimated species richness was higher for vegetation-dwelling spiders than ground-dwelling ones.

Table 2. Effects of methodological and ecological factors on spider species richness (GLM).

Strata tested	Variable tested	Source of variation	F	df	P
Vegetation	Richness	Model 1 (test for interaction)			
		Method	0.7	1	0.391
		Habitat	30.7	1	3.079e⁻⁷
		Period	0.7	1	0.391
		Method x habitat	2.1	1	0.152
		Method x period	0.7	1	0.394
		Habitat x period	0.2	1	0.650
		Method x habitat x period	0.2	1	0.652
		Model 2 (no interaction)			
		Method	0.7	1	0.389
Ground (litter)	Richness	Model 1 (test for interaction)			
		Habitat	0.3	1	0.613
		Period	0.3	1	0.613
Ground vs. vegetation	Richness	Model 1 (test for interaction)			
		Habitat x period	0.2	1	0.641
		Model 2 (no interaction)			
Habitat	0.3	1	0.61		
Period	0.3	1	0.61		
Ground vs. vegetation	Richness	Model 1 (no interaction)			
		Strata	160.8	1	<2.2e⁻¹⁶

**Fig. 1:** Comparison of species rarefaction curves between beating (A) and sweep netting (B) obtained with seven non-parametric estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2 and Bootstrap). Obs. Sr: observed species richness.

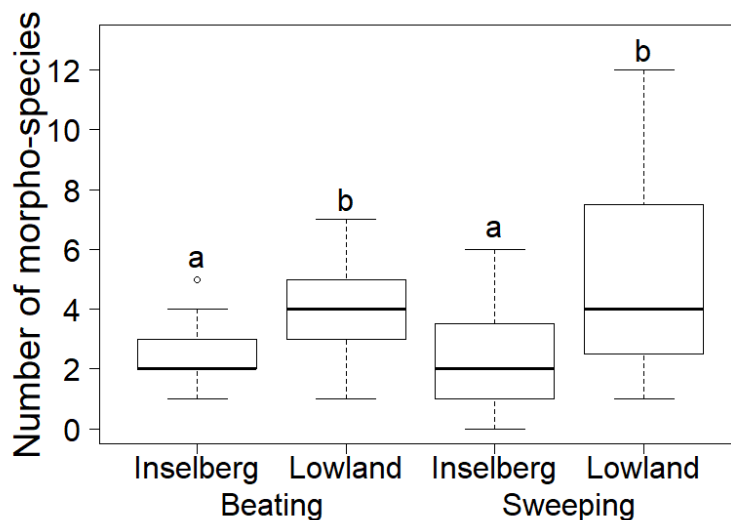


Fig. 2: Comparison of mean observed species richness between lowland and inselberg habitats, for each vegetation sampling method

Table 3: Observed and estimated species richness for the four sampling methods in both habitats. Obs.: observed.

		Obs.	Chao1	Chao2	Jack1	Jack2	ACE	ICE	Bootstrap
Inselberg	Beat	44	190	186	84	115	184	169	62
	Sweep	38	146	121	73	98	103	126	54
	Pitfall	12	22	22	19	23	35	33	15
	Litter	14	50	52	27	38	105	107	19
Lowland	Beat	66	269	303	122	166	223	239	91
	Sweep	80	252	257	150	199	230	244	113
	Pitfall	4	9	10	8	11	9	10	5
	Litter	17	39	51	32	44	57	81	23

Influence of methods, habitat, daytime and strata on composition

Difference in morpho-species composition between sweeping and beating was non-significant (PERMANOVA, $R^2 = 0.01$, $P = 0.51$).

Significant difference in morpho-species composition was found between inselberg and lowland vegetation-dwelling assemblages (PERMANOVA, $R^2 = 3.14$, $P = 1e^{-4}$). There were 176 morpho-species identified in vegetation samples (Table S1). Among them, only 19 were shared by inselberg and lowland assemblages (*i.e.* 11%), 51 were specific to inselberg (*i.e.* 29%) and 106 to lowland (*i.e.* 60%). Morpho-species belonging to the families Mimetidae and Uloboridae were only found on the inselberg while those belonging to Ctenidae and Linyphiidae were found only in lowland (Fig. 4). But the main morpho-species difference between both habitats was primarily due to four of the richest families: Theridiidae, Salticidae, Thomisidae and Araneidae. In fact, 78% of Theridiidae were specific to lowland, 11% shared to both habitats and 11% specific to inselberg. As well as 63% of Salticidae were specific to lowland, 13% common and 25% specific to inselberg; and respectively 60%, 29%, 13% of Thomisidae and 57%, 12%, 31% of Araneidae. On the contrary, there was no significant

difference in morpho-species composition of ground-dwelling samples (PERMANOVA, $R^2 = 0.045$, $P = 0.21$), but only one morpho-species was common to lowland and inselberg litter ground samples (Table S2).

There was no significant difference between day and night morpho-species abundances (*i.e.* composition) between day and night for vegetation-dwelling (PERMANOVA, $R^2 = 0.01$, $P = 0.52$) and ground-dwelling assemblages (PERMANOVA, $R^2 = 0.05$, $P = 0.11$).

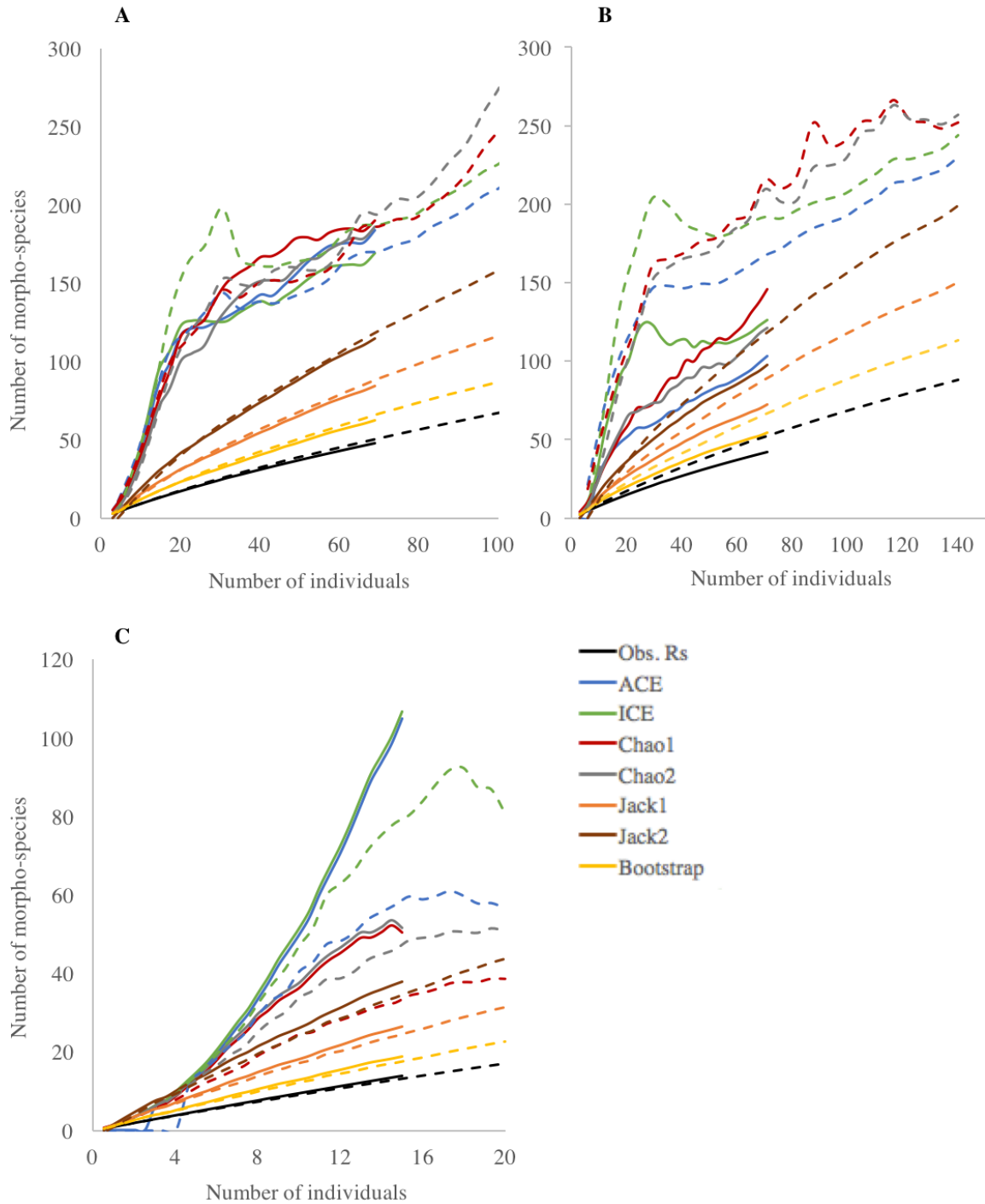


Fig. 3: Comparison of species rarefaction curves between inselberg (solid line) and lowland (dotted line) habitats obtained with seven non-parametric estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2 and Bootstrap) for 3 different sampling methods: sweep netting (A), beating (B) and litter sifting (C).

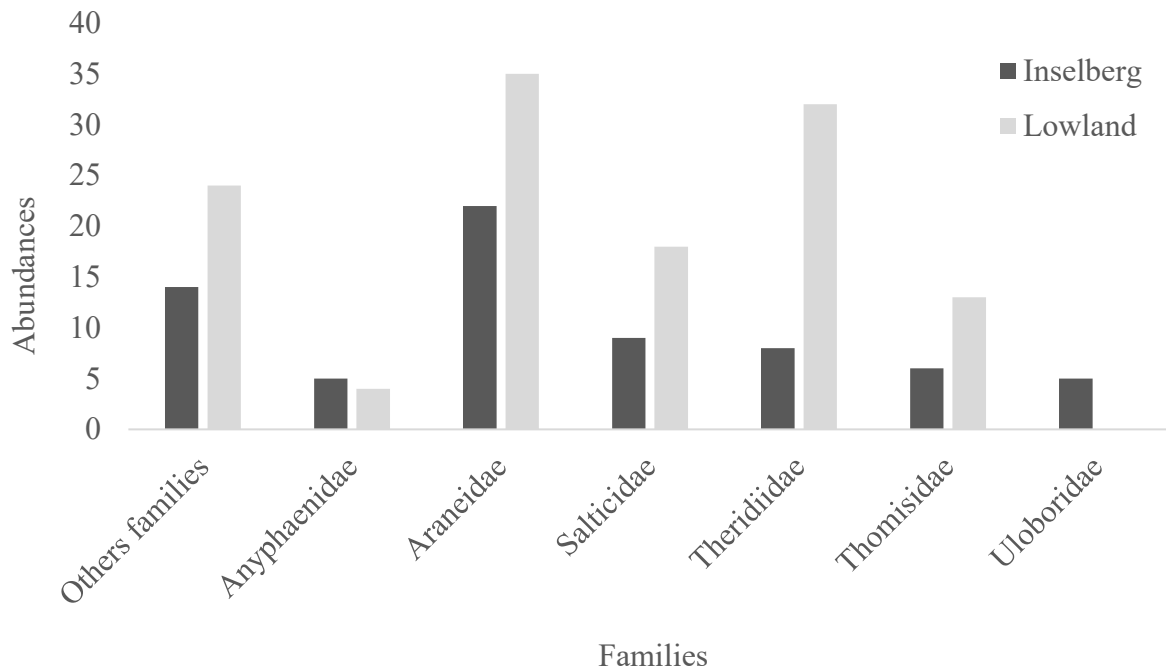


Fig. 4: Comparison of abundances by spider family between inselberg and lowland forest (vegetation samples only).

Discussion

The present study is the first application of a quasi-optimised protocol developed to answer ecological questions about tropical arthropod assemblage, particularly to compare unknown inselberg's assemblage to the little better-described lowland's. Thanks to an intensive field survey, we can bring both ecological and methodological insights by using a highly diversified group, spiders, as a model. Despite a high sampling effort, the sampling intensity is still low and the proportion of singletons is high (*sensu* Coddington et al. 2009). This typically shows the difficulty to reach exhaustive inventory, which was not our objective, when targeting mega-diverse taxa like spiders.

Comparison of sampling efficiency between methods

When doubling the volume of habitat sampled (here two times higher by sweeping than by beating), the observed species richness of vegetation-dwelling spiders did not significantly increase. Sweeping allowed to collect more individuals, but not more species. Instead, a doubled habitat volume did not increase the sampling efficiency. That is invalidating our first hypothesis: species richness does not linearly increase with the volume of habitat sampled. According to Rosenzweig (1995), species richness can logarithmically increase with sampling area. Hence, it would probably be necessary to increase the volume of habitat sampled more than expected to get a significant increase in species richness. Moreover, none of the species rarefaction curves reached an asymptote, which shows that the sampling effort was not

sufficient for both methods to collect a representative part of the spider fauna. In addition to the low abundance of most of the morpho-species collected, this suggests that the scale at which sedentary tropical arthropods should be sampled is frequently underestimated (Chao et al. 2009; Coddington et al. 2009), probably due to aggregate patterns of fauna in tropical forests. On the other hand, this absence of significant difference between sweeping and beating species richness could also be related to the fact that these methods sampled different subsets of spider assemblages, i.e. lower understory vegetation for sweep netting and higher for beating (Cardoso et al. 2008; Scharff et al. 2003; Vedel & Lalagüe 2013). However, we found no difference of composition between these two sampling methods.

Pitfall traps collected only a few ground-dwelling spiders while litter sifting collected much more. We found no correlation between species richness by pitfall traps and spatially paired litter sifting samples and no correlation between the number of individuals by both methods, i.e. abundances (pitfall traps) and densities (litter sifting). Thus, pitfall sampling cannot be considered as a surrogate of litter sifting. Pitfall traps seem to be not suitable to estimate abundance and diversity of ground-dwelling predators like spiders in tropical rainforests, which conforms to few previous studies on spiders (Azevedo et al. 2014; Luff 1975; Maelfait & Baert 1975; Malumbres-Olarte et al. 2017) and Neotropical harvestmen (Tourinho et al. 2014). Three alternative explanations can be proposed to explain this result. (i) Pitfall traps samples collected fewer spiders because they do not capture cursorial spiders. But then densities by litter sampling would have been even higher: thus, this explanation is considered unlikely. (ii) Another explanation is that pitfall traps are less efficient than the active ground sifting method because ground-dwelling spiders have low mobility. This has been suggested in temperate forests by Siewers et al. (2014) for small, web-building species. (iii) It has been previously suggested that systematic and standardized designs may not adequately reflect the abundance and composition of spider assemblages because of environmental gradients and microhabitats (e.g., presence or absence of herb layer) that are not correctly encompassed by pitfall sampling (Cardoso et al. 2009; Sereda et al. 2014). Our results showed that pitfall traps do not allow to collect a high number of spiders in tropical habitats, and we thus consider this method as unsuitable for such tropical habitats (to the difference of temperate, arctic and Mediterranean habitats where it is more effective and commonly used: see e.g., Cardoso et al. 2008; Scharff et al. 2003). This lack of efficiency should be considered to standardize further samplings of tropical ground-dwelling spiders.

Comparison of spider assemblages between inselberg and lowland forests

Inselberg forests are isolated on a rocky outcrop, characterized by harsh microclimatic conditions, poor and shallow ground, and the vegetation found there is poorer than that of surrounding, lowland, rainforests (Porembski 2007). Although the importance of inselberg forest biodiversity has been shown for vertebrates and plants (e.g., Fredericksen et al. 2003; Girão et al. 2010; Porembski 2007), we found only three studies that investigated the difference of arthropod richness and composition between lowland tropical rainforest and low forests located on the top of adjacent inselbergs (canopy spiders: Russell-Smith & Stork

1994; ground-dwelling Scarabaeidae: Feer, 2013; ground and understory spiders: Vedel & Lalagüe 2013). In their study, Vedel & Lalagüe (2013) compared the abundance, richness and diversity of spiders between one inselberg forest plot and three lowland forest plots. They found greater species richness in lowland forests spiders than in the low inselberg forest, which was explained by the differences in local habitat conditions (mainly higher moisture in lowland forests) between habitats. Feer (2013) observed the same pattern regarding the ground dwelling Scarabaeidae. However, Vedel & Lalagüe's work was a pilot study with methodological and inventory objectives undertaken with non-optimal conditions (i.e. low sampling effort, sampling during periods of low abundance for arthropods), with no spatial replication and the authors did not perform statistical tests on their data. In some Indomalayan rainforests, Russell-Smith & Stork (1994) found an increase in canopy spider abundance and richness with increasing altitude. Yet the fact that the spiders they studied were located in another biome and the canopy makes their results hard to compare to ours.

The present study partially confirmed Vedel & Lalagüe (2013) results, and supplemented them in terms of assemblage composition, also indicating contrasted results between strata. As a matter of fact, observed and estimated species richness of vegetation-dwelling spiders were higher in lowland forests than on the top of inselberg, but an opposite pattern was found for ground-dwelling spiders estimated species richness using litter sampling. Litter depth has generally direct and positive effects on spider assemblages (Uetz 1979), as well as for the ground-dwelling arthropods of tropical lowland rainforests (Ashford et al. 2013). This is overall consistent with a bottom-up control of spider density and diversity (e.g., Bennett 2010). However, we found that ground-dwelling spiders were not poorer on inselberg where the ground is shallow. We assumed three alternative and non-exclusive explanations for this pattern: (i) ground hygrometry and periodic flooding could be more limiting for the ground-dwelling spiders of lowland forests than the harsh climatic conditions and shallow ground on the Inselberg and (ii) flooding in lowland forest is a factor of litter homogenization (Adis & Junk 2002; Decaëns et al. 2016; Lafage & Pétilion 2016), which could result in decreased spider abundance and richness there. Moreover, (iii) inselberg are considered as functional islands (Prance et al. 1996; Sarthou et al. 2017) and low forests growing are more seen as ecotone (Sarthou et al. 2010) that would generate rainforest biodiversity thanks to environmental heterogeneity (Smith et al. 1997). While the species composition was studied in Vedel & Lalagüe (2013) only in lowland tropical rainforests, our study gives for the first time knowledge about spider assemblage composition on an inselberg, and its comparison to the spider composition of an adjacent lowland forest provided. The change in morpho-species composition observed in vegetation-dwelling spiders supports the idea that inselbergs act as a habitat very distinct from the surrounding forests. These tropical forest habitats host different spider assemblages, with for example less Theridiidae than in lowland suggesting that the vegetation structure complexity is lower in this habitat (Hatley & Macmahon 1980). However, morpho-species occur in low numbers. Accordingly, further studies are needed to investigate a gradual shift in composition from lowland to the top of inselbergs. Furthermore, no difference of observed diversity nor composition between habitats was found for ground-

dwelling spiders, probably because the number of individuals was too low. Nonetheless, another study conducted at the same place on ground-active Ctenids found differences in spider densities between elevations using hand-collections in depletion quadrats (Pétillon et al. 2018).

Influence of day-time collecting

Several tropical studies revealed a higher spider richness at night (Coddington et al. 1991; Green 1999; Sørensen et al. 2002) and a change in species composition between day and night (in tropical: Malumbres-Olarte et al. 2017; Sørensen et al. 2002; temperate: Cardoso et al. 2008). It has consequently been argued that spiders should be sampled both day and night in temperate and tropical forests (see Cardoso et al. 2009 and Vedel & Lalagüe 2013, respectively).

Conforming few other studies, our results showed no difference in spider species richness (see Coddington et al. 1996; Dobyns 1997 and Vedel et al. 2015 for temperate and tropical forests, respectively) and composition (see Cardoso et al. 2008 & Sørensen et al. 2002; Malumbres-Olarte et al. 2017 for temperate and tropical forests, respectively) between sampling times. Vedel et al. (2015) suggested that collecting spiders at only one time during the day was enough to estimate the diversity of spider assemblages across vegetation types. However, the lack of consensus emerging from the different studies on species composition implies that it is necessary to collect spiders during both day and night to confirm that period has no significant influence on the composition. Furthermore, sampling during both periods is still necessary to describe and inventory the diversity of spider assemblages (Malumbres-Olarte et al. 2017).

Due to the poor abundances collected by pitfall traps, comparison during both periods has only been conducted on assemblage collected by litter sifting. Ground-dwelling assemblages were then not significantly different between sampling periods. Litter sifting can only catch spiders when they are out of their refuge. Unlike what is usually reported on spider species inhabiting the leaf litter (Vedel et al. 2015), our results showed that these spiders are not more active (i.e. foraging) at night.

However, we cannot rule out the possibility that the absence of difference can be due to the low numbers of individuals collected here and generally in tropical samples because it probably had a direct influence on the assemblage composition.

Comparison of spider assemblages between ground and vegetation strata

Estimated species richness was much lower at the ground surface compared to the surrounding vegetation (data from the same sampling stations by beating and sweep-netting). Such a difference between ground and vegetation strata is surprising because their diversities are likely correlated in arthropods (Donoso et al. 2010, but see Mathieu et al. 2009 with low spider densities in an Amazonian grassland). Moreover, ecological comparisons of ground- and vegetation-dwelling spider assemblage conducted in this study highlighted that ground and

vegetation patterns in species richness are different. Vegetation-dwelling spider richness was indeed lower on the inselberg compared to the lowland forest and composition changed between both habitats, whereas observed species richness and composition did not change between habitats for ground-dwelling and estimated species richness was higher in inselbergs. These results suggest that species richness is probably not correlated between ground- and vegetation-dwelling spiders. Considering that the number of species living together reflects the richness of adaptive opportunities, species richness is the result of inter-specific competition and factors that conditioned productivity, as well as niche size, the quantity of resources (Ricklefs 1979). Hence, lowered abundances and species richness of ground-dwelling spiders would reflect a high competition with other predators such as ants, one of the most diverse taxa on tropical ground and low available resources due to a high rate of recycling (due to ants or environmental conditions) (Ashford et al. 2013; Malumbre-Olarte et al. 2017). Accordingly, ground and vegetation samples are not redundant and both are essential to fully understand the influence of ecological factors in shaping spider assemblages.

Overall, we showed that differences in the volume of sampled vegetation did not significantly influence spider species richness probably due to differences in spider assemblages sampled by both methods used. This study showed that pitfall trap-based method is uncorrelated to litter sifting and, unknnot suitable to sample ground-dwelling spiders, probably due to a too high (large spiders) or too low (small species) mobility. The habitat type (i.e. lowland vs. inselberg) influenced the species richness and composition of tropical vegetation-dwelling spiders, probably due to harsher conditions on inselberg (no pattern was found for ground-dwelling spiders). This study is, to our knowledge, the first to compare the composition of spider assemblages between lowland and inselberg forests using a standardized and statistically robust protocol. We showed the originality of inselbergs when compared to adjacent, lowland, assemblages, and bring out the basis for further studies on inselberg spider assemblages. The sampling period did not significantly influence the species richness of vegetation and ground-dwelling spiders, not more than the composition of assemblages, the latter being inconsistent with usually defined hunting guilds. Finally, by comparing vegetation and ground-dwelling spider assemblages, we showed that their diversities were not correlated and that they differently responded to ecological factors such as habitat type. Further studies are needed to understand inselberg spider diversity, test some better-standardized ground sampling in tropical rainforest, and assess the importance of other ecological factors such as vegetation structure, biomass, litter depth or prey density. Finally, this study suggests some particularities of spider assemblage structure and composition compared to the literature which is largely based on temperate habitats. It is thus urgent to compare factors shaping arthropod diversity and composition between tropical and habitats and using similar protocols.

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Supporting Information**Table S1.** Relative abundance of morpho-species collected in vegetation in inselberg and lowland forests (sweeping and beating).

Family	Morpho-species code	Inselberg (%)	Lowland (%)
Anapidae	Ana1	-	0.4
	Ana2	-	0.4
Anyphaenidae	Any1	0.8	1.7
	Any5	4.7	-
	Any6	1.6	-
	Any7	0.8	-
	Any10	-	0.4
	Any11	0.8	-
	Any12	-	0.4
	Any13	-	0.4
Araneidae	Ara2	5.5	-
	Ara4	0.8	-
	Ara10	0.8	-
	Ara11	0.8	-
	Ara13	1.6	-
	Ara15	0.8	-
	Ara19	0.8	-
	Ara20	1.6	-
	Ara21	0.8	-
	Ara22	0.8	-
	Ara23	0.8	1.3
	Ara24	-	0.4
	Ara25	-	3.9
	Ara26	-	0.4
	Ara28	0.8	0.4
	Ara30	-	0.4
	Ara31	-	0.9
	Ara33	-	2.2
	Ara34	-	0.9
	Ara35	-	0.4
	Ara36	-	0.4
	Ara37	-	0.4
	Ara39	-	0.9
	Ara40	-	1.3
	Ara41	-	0.9
	Ara42	0.8	0.4
	Ara45	-	0.4
Ara46	-	0.4	
Ara47	-	0.4	
Ara48	-	0.4	
Ara49	-	0.4	
Ara50	-	0.4	
Ara51	0.8	-	

Family	Morpho-species code	Inselberg (%)	Lowland (%)
	Ara52	0.8	-
	Ara53	0.8	0.4
	Ara54	0.8	-
	Ara55	0.8	-
	Ara57	0.8	-
	Ara58	0.8	0.9
	Ara59	-	0.4
	Ara60	-	0.4
	Ara61	-	0.4
	Ara62	-	0.4
	Ara63	-	0.4
	Ara66	-	0.4
	Ara67	0.8	0.4
	Ara69	3.1	-
	Ara70	-	0.4
	Ara72	-	0.9
	Ara73	-	0.4
	Ara74	-	0.4
Clubionidae	Clu2	-	0.9
	Clu3	0.8	-
Corinnidae	Cor3	-	5.2
	Cor4	0.8	-
	Cor5	-	0.4
	Cor7	-	0.4
Ctenidae	Cte3	-	1.3
	Cte4	-	0.9
	Cte5	-	0.9
Linyphiidae	Lin5	-	0.4
Mimetidae	Mim2	0.8	-
	Mim3	0.8	-
	Mim4	0.8	-
	Mim9	0.8	-
Nesticidae	Nest1	-	0.4
Oonopidae	Oon1	2.4	-
	Oon3	-	1.3
	Oon5	-	0.9
Pholcidae	Pho2	0.8	-
Scytodidae	Scy1	2.4	-
Salticidae	Amycus sp1	0.8	1.7
	Chira_sp1	-	0.4
	Chira_sp3	-	0.4
	Cotinusa_sp2	-	0.4
	Cylistella_sp1	7.9	3.9
	Cylistella_sp2	3.9	-
	Eustiromastix_guianae	0.8	-
	Gen14_sp1	-	0.4
	Gen18_sp1	0.8	-
	Gen19_sp2	0.8	-

Family	Morpho-species code	Inselberg (%)	Lowland (%)
	Gen20_sp1	-	0.4
	Hypaeus_sp2'	-	1.7
	Hypaeus_taczanowskii	4.7	2.2
	Lyssomanes_longipes	-	0.9
	Lyssomanes_sp5	-	0.4
	Mago_longidens	-	2.2
	Neogus_sp10	-	0.4
	Noegus_sp9	0.8	-
	Scopocira_sp1	-	0.9
	Sidusa_sp1	-	0.4
	Soesilarishius_aurifrons	-	0.4
	Soesilarishius_ruizi	-	0.4
	Soesilarishius_sp1	-	0.4
	Zuniga_magna	2.4	-
Sparassidae	Spa1	0.8	-
	Spa2	0.8	-
	Spa4	0.8	-
Synotaxidae	Syn3	-	0.9
	Syn7	-	0.4
Tetragnathidae	Tet3	0.8	-
	Tet4	-	2.2
	Tet6	0.8	-
	Tet7	-	0.4
	Tet9	0.8	0.4
	Tet10	-	0.4
Theridiidae	Ther4	0.8	0.4
	Ther5	0.8	0.9
	Ther8	-	1.3
	Ther10	3.9	0.9
	Ther12	0.8	-
	Ther16	-	2.2
	Ther17	-	0.4
	Ther18	0.8	3.1
	Ther20	-	0.9
	Ther21	-	0.9
	Ther22	-	0.4
	Ther23	-	0.4
	Ther24	-	0.4
	Ther25	-	0.4
	Ther29	-	0.4
	Ther30	-	0.4
	Ther32	-	0.4
	Ther39	-	0.4
	Ther41	-	0.4
	Ther42	-	0.4
	Ther43	-	0.4
	Ther45	-	0.4
	Ther46	-	0.4

Family	Morpho-species code	Inselberg (%)	Lowland (%)
	Ther48	0.8	-
	Ther50	0.8	-
	Ther51	0.8	-
	Ther55	-	0.9
	Ther56	-	0.4
	Ther57	-	0.4
	Ther59	-	0.4
	Ther60	-	0.9
	Ther61	-	0.4
	Ther62	-	0.4
	Ther63	-	0.4
	Ther64	-	0.4
	Ther65	-	0.4
Theridiosomatidae	Therio2	-	0.4
	Therio3	-	0.4
Thomisidae	Tho2	0.8	0.4
	Tho3	2.4	3.1
	Tho4	0.8	0.4
	Tho9	-	3.1
	Tho11	-	0.4
	Tho15	-	0.4
	Tho16	-	0.4
	Tho17	-	0.4
	Tho18	-	0.9
	Tho19	-	0.4
	Tho22	-	0.4
	ThoA	-	0.9
	ThoB	6.3	0.9
	ThoC	2.4	-
	ThoG	0.8	-
Uloboridae	U1	1.6	-
	U3	0.8	-
	U5	0.8	-
	U8	0.8	-
	U9	0.8	-

Table S2. Relative abundance of ground-dwelling morpho-species collected by litter sifting in inselberg and lowland.

Family	Morpho-species code	Inselberg	Lowland
Anapidae	Ana1	-	10%
	Ana2	-	5%
Araneidae	Ara33	7%	-
	Ara76	7%	-
	Ara77	7%	5%
	Ara78	-	5%
Corinidae	Cor8	-	5%
	Cor9	-	5%
Ctenidae	Cte19	7%	-
	Cte21	-	5%
Dipluridae	Diplu1	-	10%
Linyphiidae	Lin6	7%	-
	Lin7	-	5%
Oonopidae	Oon11	-	5%
Palpimanidae	Palp2	7%	-
Pholcidae	Pho5	-	5%
	Sa22	7%	-
	Sa27	7%	-
	Sa33	7%	-
	Sa40	7%	-
	Sa48	13	-
	Sa51	7%	-
Salticidae	Sa55	7%	-
	Ther68	7%	-
	Ther69	-	5%
	Ther70	-	5%
	Ther71	-	5%
	Ther72	-	10%
	Ther73	-	5%
	Ther74	-	5%

PART II: COMPLEMENTARITY OF TRAITS AND TAXA DIVERSITIES TO UNDERSTANDING PATTERNS OF TROPICAL SPIDERS

HOW CAN THE TRAIT-BASED APPROACH HELP IN UNDERSTANDING THE DIVERSITY PATTERNS OF TROPICAL SPIDERS?

CHAPTER.3

Comparative patterns in taxonomic and functional spider diversities between tropical vs. temperate forests

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Abstract

High diversity in tropical compared to temperate regions has long intrigued ecologists, especially for highly speciose taxa like terrestrial arthropods in tropical rainforests. Previous studies showed that arthropod herbivores account for much tropical diversity, yet differences in the diversity of predatory arthropods between tropical and temperate systems have not been properly quantified. Here, we present the first standardized tropical–temperate forest quantification of spider diversities, a dominant and mega-diverse taxon of generalist predators. Spider assemblages were collected using a spatially replicated protocol including two standardized sampling methods (vegetation sweep netting and beating). Fieldwork took place between 2010 and 2015 in metropolitan (Brittany) and overseas (French Guiana) French territories. We found no significant difference in functional diversity based on hunting guilds between temperate and tropical forests, while species richness was 13–82 times higher in tropical versus temperate forests. Evenness was also higher, with tropical assemblages up to 55 times more even than assemblages in temperate forests. These differences in diversity far surpass previous estimates and exceed tropical–temperate ratios for herbivorous taxa.

Key words: alpha diversity, Araneae, deciduous trees, France, French Guiana, functional diversity, intensive sampling.

Introduction

The latitudinal gradient of diversity, that is increase in species richness with decreasing latitude, has long been recognized by the scientific community (Pianka, 1966). Gradients of diversity in various arthropod taxa from tropical to temperate and even polar ecosystems are well documented through meta-analyses (Willig et al., 2003; but see Hillebrand, 2004). Arthropods were particularly studied in tropical rainforests (the species richest terrestrial ecosystem: Miller et al., 2002) where nearly 1.5 million tropical arthropod species are currently described out of an estimated number of 2 to 7 million tropical arthropod species (Hamilton et al., 2010; Stork, 2017). Herbivorous arthropod assemblages have been extensively studied in both tropical and temperate forests with studies of diversity, species richness per plant, host specificity, and herbivory pressure. Herbivore arthropod diversity, as well as the rate of herbivory, are considered higher in tropical systems compared to temperate counterparts (Lim et al., 2015; Peguero et al., 2017), though evidence of greater host specificity is still controversial (Novotny, 2006; Peguero et al., 2017). Such gradients in herbivore diversity can be explained by underlying plant diversity, herbivore diet specialization, and plant defense. Less well studied is the possible role of natural enemies (i.e., predators and parasitoids) on herbivore arthropod diversity (Björkman et al., 2011). Latitudinal gradients in the diversity of omnivore arthropods have also been studied, mainly in ants for which assemblages are clearly species richer in tropical versus temperate systems (Jaffre et al., 2007; Jeanne, 1979). For example, canopy assemblages of ants from tropical forests are estimated to be 4 times richer than those from temperate forests (Jaffre et al., 2007). Although ants are considered the main predatory arthropods in tropical rainforests (Floren et al., 2002), they complete a large variety of functional roles (Dejean & Corbara, 2003), and their diversity thus does not reflect the diversity of predatory arthropod taxa.

Few studies have examined the latitudinal gradient of predatory arthropod diversity, while other macro-ecological patterns were investigated in these taxa (e.g., for spiders: Arvidsson et al., 2016; Finch et al., 2008; Kozlov et al., 2015; Pitta et al., 2019; Ysnel et al., 2008). To date, most of the studies focused on predation pressure, for example, highlighting that predation pressure increases when latitude decreases (Andrew & Hughes, 2005; Novotny, 2006; Rodríguez-Castañeda, 2013), but sometimes remains constant (Cardoso et al., 2011; Zhang & Adams, 2011). Lacking are studies that directly compare the diversity of tropical versus temperate for predatory arthropods (Schuldt et al., 2013), despite their strong contribution to ecosystem diversity and functioning (Björkman et al., 2011).

To the best of our knowledge, only one study has evaluated and quantified the difference of tropical versus temperate diversity in predatory arthropods. It was conducted by Basset et al. (2012) who performed a comparison of tropical and temperate forests for different trophic guilds based on data obtained independently, using different sampling protocols. They estimated that differences in predatory arthropod diversity between tropical and temperate ecosystems should be in the same range as those for herbivorous arthropods, with tropical assemblages being 2 to 8.4 times more diverse compared to temperate forest (Basset et al.,

2012). Although spiders constitute a relevant model taxon to compare predatory arthropods between temperate and tropical regions, this ratio has never been tested nor confirmed using spiders only. They are indeed one of the few taxa, if any other, that is exclusively, except for one species and occasional plant consumption by few other species (see the recent review by Nyffeler et al., 2016), composed by predatory species (Birkhofer & Wolters, 2012).

We present here the first standardized tropical–temperate quantification for vegetation-dwelling spider diversity using the same spatially and method-replicated sampling protocol. More specifically, we compared patterns of both taxonomic and functional diversities as they bring complementary information on ecological and evolutionary processes (Tucker et al., 2018). We first expected (a) correlated patterns between taxonomic and functional diversities (as previously documented in plants and vertebrates: see Tucker & Cadotte, 2013, but also in arthropods, e.g., Birkhofer et al., 2015 and Ridell et al., 2020), (b) consistently (much) more diversity and evenness in tropical compared to temperate forests due a long time of diversification processes leading to more species and traits co-existence, and (c) an order of magnitude between temperate and tropical forests in the same range than what previously reported for other arthropods, that is, diversity and evenness around 8 times higher in tropical compared to temperate forests.

Methods

Study sites

Tropical and temperate sampling were replicated in both locations and sampling methods, to increase generalization power (Willis & Whittaker, 2002).

The two replicated tropical sites were two nature reserves in French Guiana (South America) sharing similar climates: La Trinité Reserve (76,900 ha; 4°35'2"N, 53°18'1"W) and Nouragues Reserve (105,000 ha; 4°04'18"N, 52°43'57"W). These sites are seasonally flooded rainforests with representative vegetation of the primary lowland rainforest, with few inclusions of palmetto–swamp forests, liana forests, and bamboo forests. Both forests were sampled during the rainy season, considered as the period of maximum diversity in tropical forests (e.g., Gasnier & Höfer, 2001). La Trinité and Les Nouragues were hereafter called tropical forest one and tropical forest two, respectively.

Temperate sites were in two forests preserves of mixed hardwood forests in Brittany (Western France): the forest of the military camp of Saint-Cyr-Coëtquidan (2,000 ha; 47°57'50"N, 2°11'30"W) and the state-owned forest of Rennes (3,000 ha; 48°11'53"N, 1°33'22"W). The vegetation of these forests is representative of many temperate forests with some shrubby species, small trees, and climbing plants. Only forest types dominated by native deciduous trees were sampled. Both forests were sampled in summer, the period estimated to have maximal spider diversity (see Hsieh & Linsenmair, 2012). Saint-Cyr-Coëtquidan and Rennes were hereafter called temperate forest one and temperate forest two, respectively.

While the actual sampled area was similar in all four forests, we consider the size of studied forests to be a confounding factor and an intrinsic part of the difference between tropical and temperate forests, as there are anyway no temperate forests as big as the Amazonian forest, to which the two tropical Nature Reserves sampled here belong. Tree species richness is also an intrinsic difference between the forests in each biome, with around 150 species in both Trinité and Les Nouragues tropical forests (see Guitet et al., 2018 and Poncy et al., 1998, respectively), and 10 times less in Rennes and Coëtquidan temperate forests (V. Jung comm. pers. and Morel et al., 2020, respectively).

Sampling and identification

We developed a quasi-optimal protocol (sensu Malumbres-Olarte et al., 2017 who defined it as a “standardized protocol that may not be optimal for any specific site alone.”) designed for short and intensive surveys. In each forest, we used two surface-standardized active sampling methods highly efficient for vegetation-dwelling spiders (Coddington et al., 2009): beating and sweep netting. Vegetation beating was conducted in 9 × 9 m quadrats where the vegetation was beaten with a stick over a beating tray to a height of 2.5 m. In each forest, 12 randomly selected quadrats were conducted by four people in two duos concurrently (six quadrats per duo). Sweep netting was carried out with a sweep net along 20 m long and one-meter-wide (arm length plus sweep handle) transects. Twelve randomly selected transects were conducted in each forest by the same two persons. All quadrats and transects were carried out in visually homogeneous areas of each forest that differed between methods. Tropical forest one was sampled 3–7 December 2010, tropical forest two, 6–15 December 2013, temperate forest one, 15–16 June 2015, and temperate forest two, 22–23 June 2015. Temperate adult spiders were sorted and identified to species, while tropical adult spiders were identified to morphospecies because of a lack of taxonomic knowledge in the tropics (Scharff et al., 2003). Whenever possible, males and females were matched together and grouped into one single morphospecies. All specimens were identified by the authors and stored at the University of Rennes 1, France.

Data analysis

Because of limited information for tropical spiders, functional metrics were based on the abundance of family hunting guilds only (Cardoso et al., 2011), using FD R package on the Gower dissimilarity matrix with a Cailliez correction (Laliberté et al., 2014).

The difference between functional diversity and evenness observed in each biome with each sampling technique was assessed using a mixed linear model with a Gaussian distribution. Functional diversity and evenness were the response variables, and biome and site were the predictors (respectively, fixed and random factors). The normality of results was checked using diagnostic plots. We standardized the comparison of taxonomic diversity between the four forests by using species rarefaction and extrapolation curves based on sample coverage (Chao et al., 2014). Analyses were completed using the R-based iNEXT

package (Chao et al., 2014) with R Software (R Development Core Team, 2018) on summed species abundances over the 12 replicates per method and per site. iNEXT function was configured at 40 knots and 200 bootstraps replications. 95% confidence intervals (CI) were calculated for the three measures of species diversity (species richness, Shannon, and Simpson diversity indices) within an overlap of CI used to indicate a significant difference at a level of 5% among the expected diversities (Chao et al., 2014). Diversities were compared at the same sample coverage (named “base coverage”), following Chao et al. (2014), allowing for a standardized comparison of spider assemblage diversity between biomes despite differences in forest areas. Comparisons were conducted at 38.8% sample coverage for beating and at 60% sample coverage for sweep netting.

Results

A total of 2,846 individuals belonging to 202 (morpho-)species were collected (see the detailed taxonomic list: Table S1).

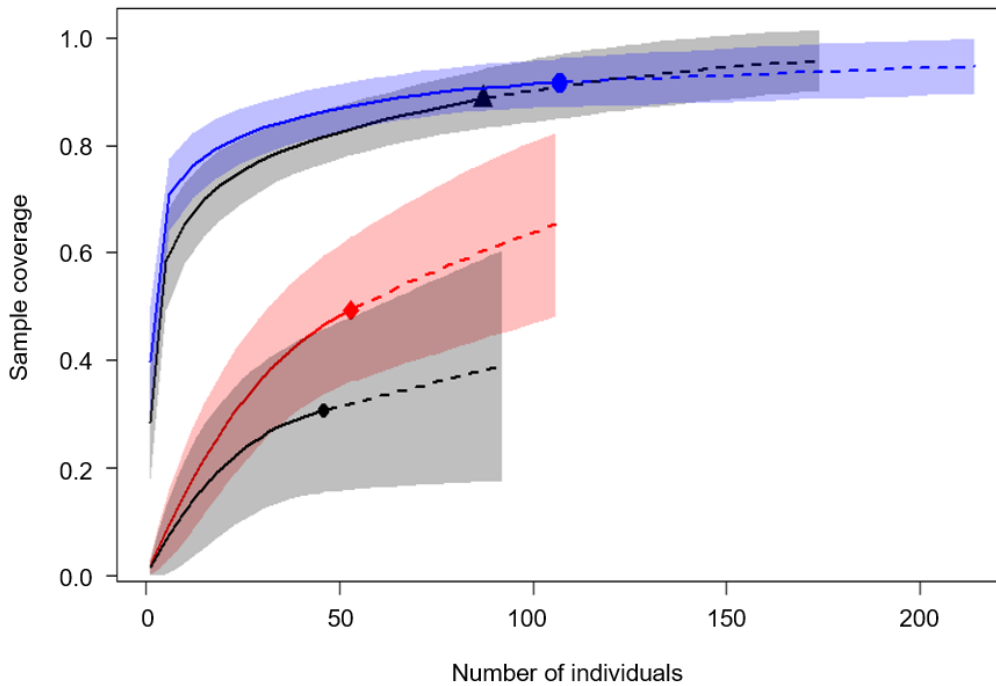
No significant differences were found between models of functional diversity based on beating sampling ($t = -0.082$, $df = 1.3$, $p = .529$) or based on sweep netting ($t = 26.06$, $df = 1.9$, $p = .195$), indicating an absence of a biome effect. The same was found for functional evenness, that is, no significant effect of biome on this metric by beating ($t = 0.79$, $df = 1.92$, $p = .515$) and by sweep netting ($t = 2.84$, $df = 1.96$, $p = .107$).

Based on rarefaction, the sample coverage was nearly two times higher in temperate forests for the two sampling methods and almost any sample size (i.e., number of individuals; Figure 1a, b). When comparing samples at the same effective sample size for both methods, sample coverage was about 90% in temperate and between 30% and 53% in tropical forests. Thus, even though the same standardized protocol was used in both biomes, temperate samples were two to three times more complete than tropical ones. Based on the extrapolation for both sampling methods, when the sample size was doubled, the sample coverage increased by three to seven percent for temperate forests and by nine to 16% in tropical ones (Figure 1a, b).

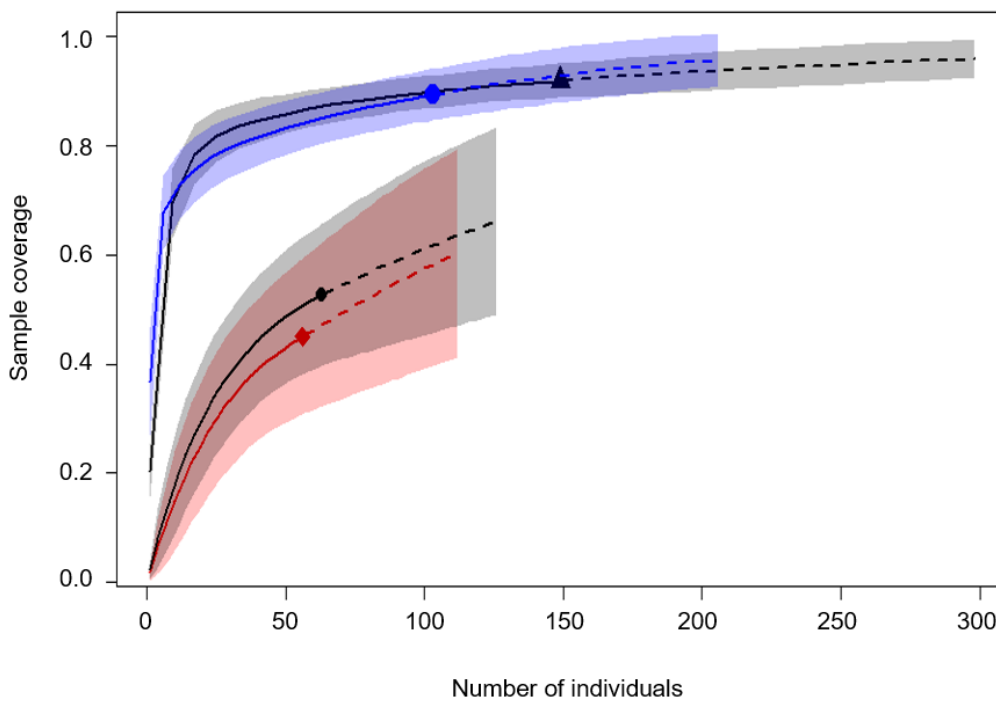
When comparing coverage-based diversities of tropical and temperate forests at the same sample coverages, confidence bands of the replicated sites of tropical and temperate forests did not overlap for either beating or sweep netting (Figures 2 and 3). Thus, tropical spider assemblages were highly and significantly more diverse than temperate ones for any sample coverage, sampling method, and diversity indices used (see detailed results below).

Beating and sweep netting consistently showed the same patterns. Tropical spider assemblages were 12.9 to 81.6 times species richer than temperate ones (Figures 2 and 3). The difference in diversity between biomes was also significant for Shannon diversity and Simpson diversity. Shannon diversity was 11.6 to 54.6 times higher in tropical assemblages than in temperate counterparts, and Simpson diversity was 10.4 to 40.4 times higher in tropical assemblages (Figures 2 and 3).

(a) Sampling method 1



(b) Sampling method 2



● Tropical forest 1 ◆ Tropical forest 2 ▲ Temperate forest 1 ● Temperate forest 2

Figure 1: Sample coverage for rarefied samples (solid line) and extrapolated samples (dashed line) as a function of sample size for spider samples collected by (A) sampling method one (beating) and (B) sampling method two (sweep netting) in tropical rainforests one and two (La Trinité and Les Nouragues) and the temperate deciduous forests one and two (Coëtquidan and Rennes). The 95% confidence intervals

are represented in light color and were obtained by a bootstrap method (Chao et al. 2014) based on 200 replications. Reference samples in each forest are denoted by solid markers. For comparison, all curves were extrapolated up to double their reference sample size. The numbers in parentheses are the sample coverage and the number of individuals for reference samples.

Discussion

Using a spatially and method-replicated protocol, we found that the taxonomic diversity of spiders was much higher in tropical forests compared to temperate forests (with consistent patterns for all diversity metrics and for the two sampling methods), when no difference was detected for functional diversity.

The fact that functional diversity was not differing among biomes can indicate either similar levels of or balanced effects of both habitat filtering and interspecific competition (Fichaux et al., 2019), which would be especially interesting at such a large spatial scale. Phylogenetic diversity can also be an interesting side of diversity, which might not be correlated with taxonomic and functional diversities as well (Tucker et al., 2018). Cardoso et al. (2011) also suspected spider taxonomic diversity to be higher in the tropics, but with species functionally redundant, which was supported by Schuldt et al. (2013) who compared tropical (China) and temperate (Germany) spider assemblages.

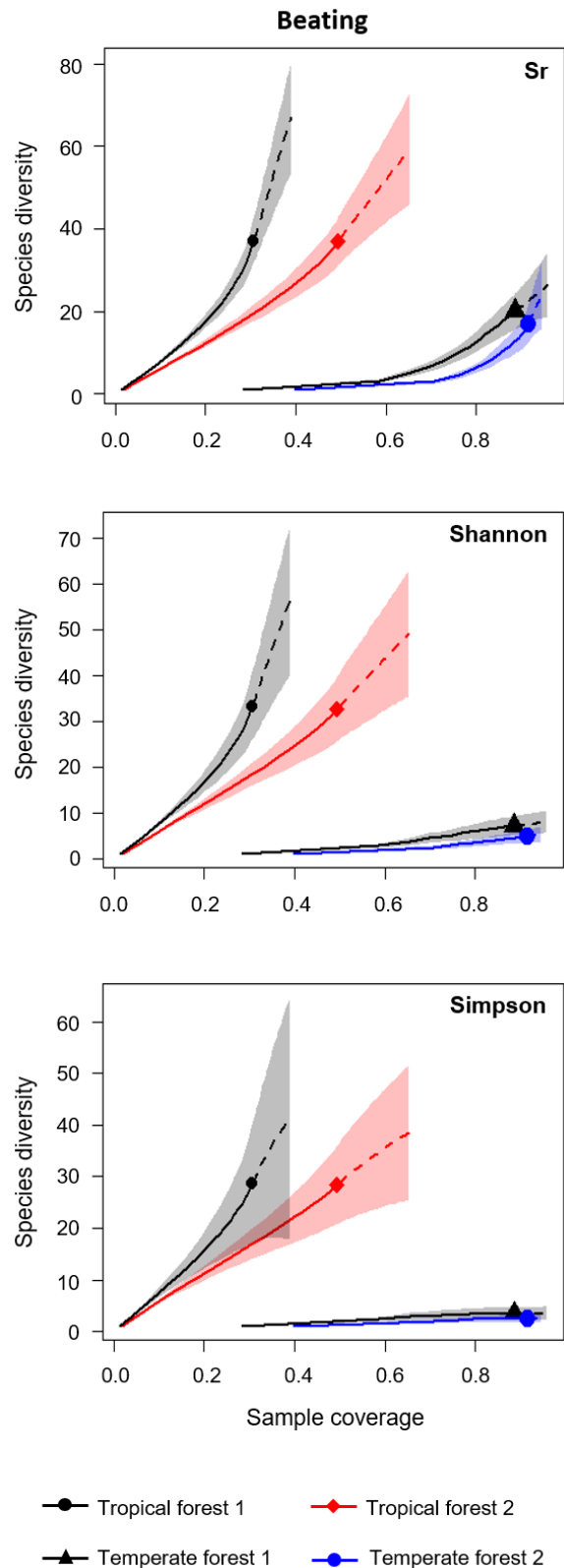


Figure 2: Comparison of the coverage-based rarefaction (solid line) and extrapolation (dashed line) of spider (A) species richness (Sr), (B) Shannon diversity and (C) Simpson diversity collected by sampling method one (beating) in tropical rainforests one and two (La Trinité and Les Nouragues) and the temperate deciduous forests one and two (Coëtquidan and Rennes). The 95% confidence intervals are represented in light color and were obtained by a bootstrap method (Chao et al. 2014) based on 200 replications. Reference samples in each forest are denoted by solid markers. For comparison, all curves were extrapolated up to double its reference sample size. The numbers in parentheses are the sample coverage and the observed diversity indices (species richness, Shannon or Simpson) for each reference sample.

The functional diversity was yet based on hunting guilds only in this study and should be computed with other traits in the future when they will be available at large spatial scales (Lowe et al., 2020).

Our study showed that, with the same level of sample coverage, species richness of tropical forest spiders was 13–82 times higher than temperate species richness. This magnitude of difference is much greater than expected (i.e., two to eight times more than in Basset et al., 2012). The comparison of evenness also revealed that the spider assemblages we sampled in tropical forests were also up to 55 times more even than in temperate forests. Weighted measures of diversity (i.e., species evenness and species dominance) are known to provide more comprehensive views of patterns of taxonomic diversity (Willig et al., 2003). Diversity metrics responded in the same way than species richness (and consistently between sampling methods), which confirms that spider diversity was up to 30 times higher than what was previously proposed for predatory arthropods through indirect comparisons.

Although several methodological factors could influence the difference in ratios between Basset et al. (2012) and this study, and among them the indirect comparison used by Basset et al. (2012), the strata sampled (understory here vs. soil to canopy for Basset et al., 2012), and the species richness estimation methods (a large range of different estimators in Basset et al., 2012) but without considering sample

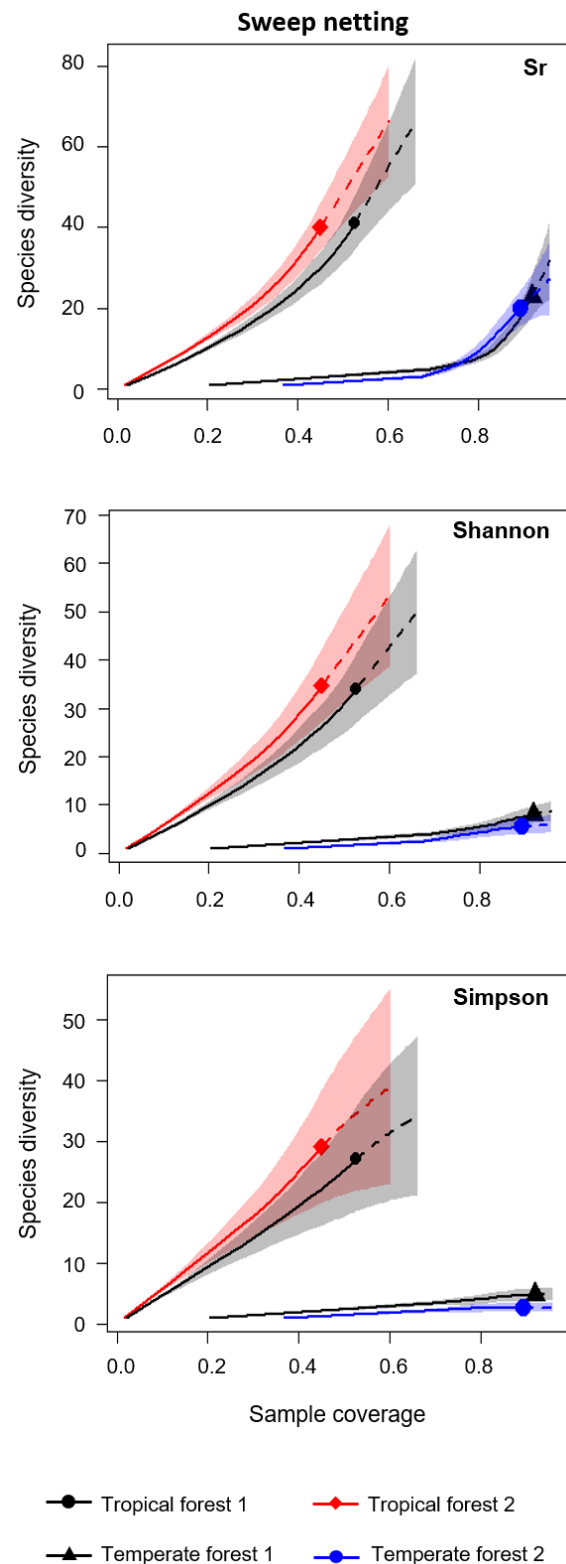


Figure 3: Comparison of the coverage-based rarefaction (solid line) and extrapolation (dashed line) of spider (A) species richness (Sr), (B) Shannon diversity and (C) Simpson diversity collected by sampling method two (sweeping) in tropical rainforests one and two (La Trinité and Les Nouragues) and the temperate deciduous forests one and two (Coëtquidan and Rennes). The 95% confidence intervals are represented in light color and were obtained by a bootstrap method (Chao et al. 2014) based on 200 replications. Reference samples in each forest are denoted by solid markers. For comparison, all curves were extrapolated up to double its reference sample size. The numbers in parentheses are the sample coverage and the observed diversity indices (species richness, Shannon or Simpson) for each reference sample.

coverage), we still argue that predatory arthropods are proportionally more diverse in tropical compared to temperate forests than other taxa, like, for example, herbivore arthropods and plants. The global difference in diversity between tropical and temperate ecosystems is indeed partly explained by both plant species richness and plant phylogenetic diversity (Dinnage et al., 2012), which suggests that the diversity of predatory arthropods also mirrors plant diversity. Interestingly, the values of tree diversity of our study sites are comparable to those of other temperate and neotropical forests (see e.g., Brokaw & Busing, 2000) and also fit to previous estimations of 5–10 times more plant species per hectare in tropical compared to temperate areas (Barthlott et al., 1996). Hence, the 13–82 times higher species richness of spiders in tropical rainforest would be vastly higher than the actual difference in tree diversity between the same pairs of forests. Thus, spiders would be 1.2 to 16 times proportionally richer than plants in tropical compared to temperate systems. These results suggest that the relationship between spider and plant diversity in tropical forest would not be one-to-one as it was previously estimated for all trophic level arthropods (Basset et al., 2012; Dinnage et al., 2012). The ratio between plant and spider diversity in tropical forests compared to temperate forests could be higher due to a wider diet of spiders in tropical versus temperate forests (see Birkhofer & Wolters, 2012 for further information). Lastly, vegetation structure, known to affect spider diversity (see e.g., Hurd & Fagan, 1992), could also have played a role in shaping differences of species richness between biomes. But understory structure, which was not quantified here, did not look so different between (primary) tropical and (secondary) temperate forests, even possibly higher in the latter (K. Privet & J. Pétilion, pers. observations).

Finally, intensive sampling in tropical regions is often limited in time and replication, which potentially induces biases such as random effects and particular local conditions. We are aware that our design would have benefited from additional replication, but there is also a risk to increase intratreatment variance by doing so in a single design (Oksanen, 2001). Therefore, we encourage tropical researchers to continue sampling spider diversity, using this or other standardized sampling protocols, in paired comparisons of tropical versus temperate forests to infer on eco-evolutionary drivers of biodiversity patterns at large spatial scales.

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Supporting information

TABLE S1: List and abundances of species collected during this study. Part of the spiders collected in tropical forests was unknown and only tropical spiders belonging to the family Salticidae were identified to the species level.

Forest			Species	Abundance
Temperate forest (Saint-Cyr-Coëtquidan)	1		Anelosimus vittatus	1
			Araneus diadematus	1
			Ballus chalybicus	2
			Clubiona compta	4
			Clubiona terrestris	1
			Diaea dorsata	2
			Dipoena melanogaster	1
			Enoplognatha ovata	102
			Episinus maculipes	1
			Gongylidium rufipes	3
			Hypomma cornutum	2
			Linyphia hortensis	2
			Mangora acalypha	1
			Metellina menegi	31
			Metellina meriane	4
			Neottiura bimaculata	2
			Neriere peltata	1
			Neriere radiata	1
			Oedothorax fuscus	2
			Paidiscura pallens	2
			Parasteatoda simulans	2
			Pelecopsis parallela	1
			Philodromus albidus	2
			Philodromus rufus	1
			Platnickina tinctoria	2
			Porrhomma microphthalmum	1
			Tenuiphantes flavipes	33
			Tenuiphantes zimmermanni	14
			Tetragnatha montana	4
			Theridion varians	2
			Theridiosoma gemmosum	4
	Zilla dioidia	4		
Temperate forest (Rennes)	2		Anelosimus vittatus	1
			Araneus diadematus	1
			Batyphantes gracilis	5
			Ceratinella scabrosa	1
			Clubiona brevipes	1
			Diaea dorsata	1
			Dipoena melanogaster	1
			Enoplognatha ovata	127
			Erigone atra	1

			<i>Erigone dentipalpis</i>	2
			<i>Hypomma cornutum</i>	1
			<i>Linyphia hortensis</i>	1
			<i>Metellina mengei</i>	17
			<i>Neriere peltata</i>	2
			<i>Nigma puella</i>	1
			<i>Oedothorax fuscus</i>	1
			<i>Oedothorax retusus</i>	1
			<i>Paidiscura pallens</i>	7
			<i>Parasteatoda lunata</i>	2
			<i>Parasteatoda simulans</i>	4
			<i>Philodromus albidus</i>	1
			<i>Philodromus dispar</i>	3
			<i>Philodromus praedatus</i>	1
			<i>Platnickina tinctoria</i>	14
			<i>Tenuiphantes flavipes</i>	5
			<i>Tenuiphantes tenuis</i>	1
			<i>Tenuiphantes zimmermanni</i>	2
			<i>Tetragnatha montana</i>	1
			<i>Tetragnatha obtusa</i>	2
			<i>Theridion varians</i>	1
			<i>Walckenaeria vigilax</i>	1
Tropical	forest	1		
(La Trinité)			AnaA	1
			AnaB	1
			AnyA	1
			AnyH	1
			AraAP	1
			AraAR	1
			AraAT	1
			AraC	1
			AraD	1
			AraE	1
			AraG	1
			AraH	1
			AraI	1
			AraJ	3
			AraL	1
			AraP	1
			AraV	1
			CluA	1
			Cobanus sp3	1
			CorA	1
			CorH	1
			CorJ	1
			CorK	1
			CorL	1
			CorM	1
			Corythalia sp4	1

Cylistella sp1	1
Erica eugenia	1
Gen9 sp1	1
Hypaeus porcatus	1
Hypaeus sp2'	3
Hypaeus taczanowskii	10
LinA	1
LinE	1
LinI	1
Lyssomanes longipes	2
Lyssomanes nigropictus	1
Lyssomanes sp3	1
Mago longidens	1
MimA	4
Noegus niveomarginatus	4
Noegus sp1	2
Noegus sp11	1
Noegus sp5	1
OxyoA	1
OxyoB	2
PhoIA	3
PisC	1
PisE	1
PisF	1
PisG	1
PisI	1
Scopocira cf tenella	3
ScyA	4
ScyB	1
ScyC	1
Soesilarishius sp1	1
TetF	1
TherAA	2
TherAF	1
TherAG	1
TherAH	1
TherAI	1
TherAJ	1
TherAK	1
TherAL	1
TherAQ	1
TherB	10
TherC	2
TherD	6
TherE	1
TherG	3
TherH	2
TherI	1

TherJ		2
TherK		2
ThoAD		1
ThoAE		1
ThoAF		2
ThoAK		1
ThoB		1
ThoC		10
ThoD		1
ThoE		6
ThoF		1
ThoH		6
ThoI		5
ThoJ		1
ThoN		1
ThoO		1
ThoP		5
ThoQ		1
UloA		2
UloD		4
UloJ		1
UloK		1
<hr/>		
Tropical forest	2	
(Les Nouragues)		
Ana2		1
Any1		1
Any12		1
Any13		1
Ara23		2
Ara25		6
Ara33		4
Ara40		2
Ara53		1
Ara58		2
Ara59		1
Ara60		1
Ara61		1
Ara62		1
Ara63		1
Ara66		1
Ara72		2
Chira sp1		1
Cor3		5
Cor5		1
Cor7		1
Cotinusa sp2		1
Cylistella sp1		7
Gen20 sp1		1

Hypaeus sp2'	1
Hypaeus taczanowskii	5
Lin5	1
Mago longidens	4
Neogus sp10	1
Nest1	1
Oon5	2
Sidusa sp1	1
Soesilarishius aurifrons	1
Soesilarishius ruizi	1
Soesilarishius sp1	1
Syn3	1
Syn7	1
Tet10	1
Tet4	2
Tet7	1
Tet9	1
Ther10	1
Ther16	1
Ther18	3
Ther21	1
Ther55	2
Ther56	1
Ther57	1
Ther59	1
Ther60	2
Ther61	1
Ther62	1
Ther63	1
Ther64	1
Ther65	1
Therio2	1
Tho15	1
Tho16	1
Tho17	1
Tho18	2
Tho19	1
Tho2	1
Tho22	1
Tho3	5
Tho9	4
ThoA	1

CHAPTER.4

Complementary of taxon- and trait-based metrics to understand tropical patterns of diversity –A case study using spider assemblages of contrasted neotropical forests habitats

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Abstract

To what extent taxonomic vs functional metrics are redundant in terms of revealing and understanding diversity patterns remains unclear, especially in purely predatory taxa. This question is highly relevant in tropical forests where arthropod assemblages reach huge species numbers and their assembly rules are still largely unknown. Using a large-scale design (gradient of forest structure repeatedly sampled in 4 sites distributed over French Guiana), we tested the redundancy between metrics of taxon- vs. trait-based diversities in spiders, a mega-diverse, yet less-studied, group of predatory arthropods. All spiders were identified to family level and then discriminated to morpho-species (described species whenever possible) based on both habitus and sexual organs to estimate taxonomic diversity (TD) to eventually compute three diversity metrics (q0-Species richness, q1-Shannon diversity, q2-Simpson diversity). Because the knowledge on traits is still scarce in spiders, we used the actual measurements of 6 biometric traits on all individuals to better estimate functional diversity (FD), together with the hunting guild of spiders (attributed to family level). We first tested for correlations between a global set of diversity metrics (3 TD vs. 4 FD) using all possible combinations of traits. We then compared the patterns of estimated TD and FD (all for q0, q1 and q2) along with the range of habitat conditions (type of forest, type of localization and site), also investigating how patterns were affected by the presence/absence of juveniles in the dataset. Our results overall showed a little influence of including or not juveniles, a little influence of q order (except for increasing correlations between FD and TD metrics), a little influence of several traits (except for hunting guilds that drove most of the FD patterns) and conversely a strong influence of forest type on both TD and FD patterns which were globally correlated. While these results suggest important environmental filtering, even in tropical forests, the precise role of abiotic factors and the influence of species and traits in composition turn-over remain to be tested. Our study finally calls for better standardization of metrics, in terms of estimated metrics, but also for more actually-measured traits in arthropod community ecology.

Key words: Araneae, environmental filtering, estimated predictors, functional traits, French Guiana.

Introduction

Determining assembly rules of co-occurring species persists as a fundamental goal in community ecology (Weiher & Keddy, 2001). Assemblage diversity is influenced by both deterministic (i.e. niche related) and stochastic (i.e. neutral) factors. From the deterministic perspective, both biotic and abiotic factors locally influence the patterns of diversity (Weiher & Keddy, 2001; Maire et al., 2012) through niche differentiation (MacArthur & Levins, 1967) and habitat filtering (Keddy, 1992), respectively. Habitat filtering limits the establishment of species unable to tolerate abiotic conditions of a given habitat, resulting in co-occurring species with similar ecological attributes (Keddy, 1992). Competitive interactions can reduce the coexistence of species sharing similar niches (MacArthur & Levins, 1967) or reinforce competitive hierarchies of species (Chesson, 2000; Kunstler et al., 2012), resulting in niche differentiation through character displacement: spatial and/or temporal partitioning of species with similar ecological attributes (Diamonds, 1975; Gotelli & McCabe, 2002). Those deterministic processes act at different spatial scales such as local and regional scales (Chase & Myers, 2011). Simultaneously, assemblages are influenced by factors that are more stochastic such as chance colonization, random extinction, and ecological drift (Chase & Myers, 2011).

Traditionally, studies investigating assembly rules across different ecosystems focused mainly on taxonomic diversity. Taxonomic diversity does not give any information on character displacement, a change that occurs when similar species inhabit the same environment, and when natural selection favors the divergence in the characters (morphology, ecology, behavior, or physiology) of the organisms. A more comprehensive functional trait-based approach has recently been formalized, which links taxonomic entities with the ecological functions they fulfill in their environment, providing a way to distinguish between assembly processes (McGill et al., 2006; Cadotte et al., 2011; Houseman & Gross, 2011; Villéger et al., 2011; Weiher et al., 2011). Integrating taxonomic and functional approaches thus provides a more comprehensive insight into the role of environmental filtering and competitive exclusion.

Arthropods are more and more investigated in ecological studies because of their huge abundance and diversity (Erwin, 1982; Scharff et al., 2003) as well as their central role in ecosystem functioning (Lamarre et al., 2012; Hamilton et al., 2013). A better understanding of the distribution patterns of arthropods is essential both to better predict the dynamics of their taxonomic and functional diversity and to manage efficiently the conservation issues related to these organisms (Novotny & Basset 2000). The majority of terrestrial eukaryote diversity on Earth is represented by arthropods in tropical rainforests (Miller et al., 2002; Hamilton et al., 2010). However, the rules that structure their assemblage across environmental gradients are still very little known (but see Lamarre et al., 2016; Fichaux et al., 2019; Privet et al., 2020). Determining how assemblages are structured across environmental gradients in tropical

environments will help to understand the mechanisms that rule hyperdiverse communities. Using the taxonomic approach is complicated in tropical assemblages due to the lack of knowledge of the species, and its only use has proven its limits to explain the patterns of diversity (e.g., Privet et al., 2018). Trait-based approaches give a complementary view of the patterns of diversity (Violle et al., 2007; Pavoine & Bonsall, 2011; Brousseau et al., 2018; Wong et al., 2019) and are increasingly being used to test mechanisms underlying assemblages (Moretti et al., 2017). Terrestrial arthropods constitute one of the most promising, but also challenging, taxa regarding community ecology (and underlying assembly rules), due to their huge taxonomic and functional diversity (Moretti et al., 2017). However, the trait-based approach is just starting to be unified for terrestrial arthropods (Brousseau et al., 2018; Wong et al., 2019; Lowe et al., 2020) and is especially hard to use in tropical environments due to the lack of knowledge in natural history including easy-to-measure functional traits. Interestingly, the growing number of studies comparing the patterns and drivers of taxonomic vs functional diversities for terrestrial arthropods show evidence for important differences among taxa (Hacala et al., 2021) and/or spatial scales (Privet & Pétilion, 2020) that prevent generalizations.

Among terrestrial arthropods, spiders (Araneae) are one of the most diversified and abundant groups with very large ecological affinities and a worldwide repartition. Due to these characteristics, spiders have been proposed as a model group for uncovering ecological patterns (Cardoso et al., 2011; Birkhofer & Wolters, 2012; Malumbres-Olarte et al., 2018). Spider assemblages are known to be determined by environmental factors (e.g., elevation, temperature, habitat structure and complexity) and biotic interactions (e.g., competition, intraguild predation, predation) in temperate ecosystems (but see Fernandez-Fournier & Avilés, 2018 for tropical habitats) assessed mostly by traditional taxonomic approach (Wise, 1993; Butler & Haddad, 2011; Gonçalves-Souza et al., 2011; Diehl et al., 2013; Malumbres-Olarte et al., 2013; Gómez et al., 2016; Mammola et al., 2016; Petcharad et al., 2016). The trait-based approach of assemblages is relatively new in spiders and has been recently taken to another level thanks to the creation of the World Spider Trait database (Lowe et al., 2020; Pekar et al., 2021a and b). The diversity of spider traits is known to be influenced by, among other factors, habitat and vegetation structure (e.g., Schirmel et al., 2012; Corcuera et al., 2016; Gallé et al., 2018). However, knowledge on their traits is for the moment still lacking because individual traits are unreported, often derived from large-scale databases (Pey et al., 2014), or vary in an unquantified way (Basset et al., 2003), including at intraspecific scale (Suter & Benson, 2014). In the case of tropical spiders, since most of them have not been described, there is really few knowledge about their trait diversity (but see Schuldt *et al.* 2014, Liu *et al.* 2015, Schuldt & Staab 2015, Pétilion *et al.* 2018). Moreover, spider traits functionality has not been explicitly tested (as for most terrestrial arthropods, Wong et al., 2019). Therefore, it is preferable to speak of trait-based diversity rather than functional diversity.

While trait-based diversity is known to be correlated to taxonomic diversity as a rule, first by mathematical effects (plants: Pavoine et al., 2013, spiders: Ridel et al., 2021), the

redundancy of taxonomic vs trait-based (functional) diversity metrics in terms of revealing and understanding diversity patterns remains unclear, especially in purely predatory taxa. In this study, we investigated the variation of taxonomic and trait-based diversities of tropical spider assemblages over a range of tropical habitats varying in vegetation structure and environmental constraints (Baraloto et al., 2011; Lamarre et al., 2016, see Material and methods for a description of the habitats). We therefore expected taxonomic and trait-based diversities to vary among habitats because of differences in environmental constraints, resource availability, plant composition and habitat structure (Lamarre et al., 2016). We present here preliminary results investigating the correlation of a set of diversity metrics, we first tested for direct correlations between three taxon-based vs. four traits-based diversity metrics using all possible combinations of seven traits (of which six were actually measured on spiders and one derived from literature). We then compared the patterns of estimated taxonomic and trait-based diversities along with the range of habitat conditions (type of forest, type of localization and site). Juveniles spiders are usually discarded from assemblage analysis due to the difficulty or impossibility to identify them (Coddington et al., 1996; Dobyms, 1997; Scharff et al., 2003). However, they constitute a significant part of the assemblages and their patterns are in some cases different than those of adults (Norris, 1999; Domènech et al., 2021) and similar in other (Jiménez-Valverde & Lobo, 2006). In tropical assemblages they can account from 40% (in Privet et al., 2020), to 67% (in Privet et al., 2018) or even 86% (in Campuzano et al., 2016). Thus we investigated the patterns of taxonomic and trait-based diversity of adults and juveniles assemblages.

Material and methods

Study sites

This study was conducted in four sites of French Guiana that represent the entire range of variation in climatic, edaphic, forest structure factors and forest habitats observed in a larger plot network in tropical forests of South America in Loreto, Peru, and French Guiana (Baraloto et al., 2011; Lamarre et al., 2016). Two sites were located along the coast of French Guiana: (1) the French Guiana Space Center (CSG) (5°13'51" N, 52°46'08" W), which is a protected that contains several habitats including diverse forests, savannahs, marshes and mangroves (CNES & ONF, 2020); and (2) Laussat (5°29'00" N, 53°34'00" W), which is mostly covered with plains forests (Guitet et al., 2015). The two other sites were located deeper inland: (3) La Trinité (4°35'20" N, 53°18'01" W) is a reserve situated on the center-north of French Guiana. It is covered with a variety of forests, crossed by a mountain range comprising multiple inselbergs (Réserve Naturelle La Trinité, 2013). (4) Les Nouragues (4°04'18" N, 52°43'57" W), is a reserve located in the center-east of French Guiana. It holds a large forest cover, rock savannahs and inselbergs (Réserve Naturelle Nouragues, 2013).

Studied habitats

We studied four of the main tropical habitats of the Amazon basin:

(1) Terra firme forests, which are the most common forest in French Guiana developing on high soil nutrient content. They are dense and stratified, with a typical forest canopy reaching 20 to 40 meters, dense shrub vegetation but a sparse herbaceous stratum (Baraloto et al., 2011).

(2) Seasonally flooded forests, which are regularly subject to inundations that submerge soil surfaces during periods of high precipitations (Baraloto et al., 2007). These repeated disturbances result in a high rate of tree fall which prevents plant succession (Ferry et al., 2010; Baraloto et al., 2011; Quesada et al., 2012). Their canopy is more open than in terra firme forests and only a few plant species are endemic to these seasonally flooded forests (Guitet et al., 2015).

(3) White sand forests, which develop over nutrient-poor and dry sandy soils. They have more open canopy than previously cited habitats and hold poorer amounts of organic matter although they have the highest wood density (Baraloto et al., 2011). White sand forests occur as habitat islands surrounded by Terra Firme and seasonally flooded forests (Fine & Bruna, 2016). They host endemic plant species (Fine et al., 2010).

(4) Inselberg forests, which grow over rocky, granitic formations so-called inselbergs. These forests are subject to harsh abiotic conditions, such as extreme temperatures or massive runoffs depleting soils of their nutrients. Inselberg forests have a dense herbaceous cover which is however dotted by sand and granite outcrops. Their vegetation is mostly composed of shrubs and thickets making their canopy widely open. Tree species richness of inselbergs forests was estimated equivalent to white sands forests tree species richness (see Baraloto et al., 2011 and Sarthou et al., 2009) but their vegetation is highly endemic (Porembski & Barthlott, 2000; Porembski, 2007; Sarthou et al., 2017).

Sampling

Fieldwork was conducted during 12 months between November 2013 and October 2015.

Spiders were sampled in 23 forests plots distributed among the four habitats (terra firme and seasonally flooded forests in all sites, white sand forests in coastal sites and inselberg forests: see Baraloto et al., 2011). Each plot consisted of ten 10*50 m transects distributed in a 2 ha area chosen for homogeneity and representativeness of the habitat (Lamarre et al., 2016), and contained at least 60 trees. Plots were at least 1 km apart to avoid interactions. Two plots were sampled into each habitat of each site, except the inselberg and the seasonally flooded forests of Les Nouragues and the inselberg forests of La Trinité where one plot was sampled, and the terra firme forest of La Trinité where three plots were sampled, resulting in a total of 23 sampling plots.

Spiders were sampled using Amazonas traps in inland sites and using hand collecting in coastal sites. Amazonas traps consist of slipping a bag onto a plant before mightily shaking the

tree to shake off the spiders, before collecting them utilizing aspirators (see Lopes et al., 2019 for details). Collected spiders were preserved in 70% ethanol and deposited at the Université of Rennes 1 (Rennes, France).

Taxonomic identification

Individuals were sorted and identified to family following to Dippenaar-Schoeman & Jocqué (1997), Adis (2001) and Jocqué et al. (2006). Due to the lack of taxonomical knowledge about tropical spiders, we thus identified spiders to morpho-species based on morphological traits, mainly by observation of genitalia and habitus. Under a 65 microscope, we realized a side-by-side comparison of specimens to determine distinct morphological entities. Both juveniles and adults were identified at the family level and tentatively at the morpho-species level when possible (down to species for salticids).

Traits selection and determination

We examined variation in hunting guilds and a suite of six morphological traits for spiders from the different forest habitats. This character set was selected a priori based on their importance to spiders use of the habitat.

Hunting guilds are non-phylogenetic groups of species that share one or a series of resources (Blondel, 2003) and may thus reflect the ecological niche of spiders. Hunting guilds were determined for families or genera according to Dias et al. (2009) and Cardoso et al. (2011) resulting in seven groups: active hunter, ambusher, stalker, ground web weaver, sheet web weaver, spatial web weaver, and orb web weaver.

Morphological traits were selected for their accessibility and their potential to reflect the use of the habitat by spiders: **leg length** may reflect efficiency in locomotion, dispersal, and web construction (Foellmer & Fairbairn, 2005; Foelix, 2010), and **body size** may reflect differences in environmental factors as it is correlated with many life history mechanisms as resource use, starvation, desiccation resistance, and other physiological processes (Cushman et al., 1993; Entling et al., 2010). In total, **six measures** were realized to the nearest 0.001 mm using the software Fiji (Schindelin et al., 2012) and a binocular loupe equipped with a Nikon SMZ800 camera. The femurs of legs 1 and 4 (from the rim of the trochanter to the junction with the patella) and tibiae of legs 1 and 4 (from the rim of the patella to the junction with the metatarsus) were measured as indicators of leg lengths. When it was possible, these two legs were measured on the right side of spiders. The length of the prosoma (measured from the middle of its anterior extremity to the middle of its posterior extremity, dorsal view) and the width of the prosoma (measured at its widest, dorsal view) were measured as indicators of body size. As both measures were strongly correlated (85.03%), we realized analyses on prosoma width only (Jakob et al., 1996). In case of a missing value (e.g., no legs), the individual received an average value of measured traits from the same morpho-species in the given plot, if any.

Diversity metrics and data analysis

As trait-based diversity is still under recent development in spiders (Lowe et al., 2020), we first tested direct correlations between taxon-based vs. traits-based diversity of the 7 possible combinations of the 3 non-correlated studied traits (hunting guilds, body size and leg length: see above). We explored the Spearman correlation of taxonomic diversity with trait-based diversity for three taxonomic diversity indexes – taxonomic richness, Shannon and Simpson diversity – and four trait-based (functional) diversity indexes – functional richness, functional evenness, functional divergence and Rao Index. (i) functional richness (FRic) indicates the amount of the functional space occupied by the community, (ii) functional evenness (FEve) describes regularity in the distribution of the community abundance within the functional trait space, (iii) functional divergence (FDiv) defines how species abundances are distributed within the functional trait space, and (iv) Rao index (RaoQ) measures dissimilarity between species divided by their relative abundances (Mason et al., 2005; Villéger et al., 2011). These trait-based diversity indexes were calculated following Botta-Dukát (2005) and Laliberté & Legendre (2010) methods, using the “dbFD” function in the “FD” package (Laliberté et al., 2014). The number of dimensions retained was equivalent to the number of species in the most species-poor community.

In a second step, we compared the patterns of taxonomic and trait-based diversities between habitats. We started by analyzing taxonomic diversity separately for inland and coastal sites. We then estimated both taxonomic and trait-based diversity (using all traits) for the pooled inland and coastal sites, and compared patterns over habitat types for adults only, juveniles only, and both. Taxonomic and trait-based diversities were estimated using rarefaction and extrapolation of hill numbers (Chao & Jost, 2012; Colwell et al., 2012; Chao et al., 2014, 2021; Hsieh et al., 2016). Hill numbers are a mathematically unified family of diversity indices that have been generalized for taxonomic and trait-based diversity (Chao et al., 2021). Hill numbers differ among themselves only by an exponent q . For taxonomic diversity, hill number of $q=0$ corresponds to the taxonomic richness; $q=1$ to the exponential of Shannon entropy (that can be interpreted as the effective number of abundant/common species); and $q=2$ to the inverse of the Simpson concentration index (that can be interpreted as the effective number of highly abundant or dominant species). For trait-based (functional) diversity, hill number of $q=0$ corresponds to the effective total number of functional groups (functional-group richness); $q=1$ to the effective number of common/abundant functional groups; and $q=2$ to the effective number of dominant or highly abundant functional groups (Chao et al., 2021). Comparisons of estimated diversities can be made at the same sample size (comparisons based on the number of individuals) or the same sampling coverage (comparisons based on the sample completeness). The sample size does not take into account the fact that some assemblages are richer than others and therefore leads to an underestimation of large assemblages (Chao & Jost, 2012). Sampling completeness represents the proportion of assemblage species represented in a sample (Chao & Jost, 2012). Comparing estimated assemblage diversity based on completeness recognizes that more diverse assemblages require greater sampling effort to be properly characterized (see Roswell,

Dushoff, & Winfree, 2021 for a review). We compared taxonomic diversities of the habitats of the coastal and inland sites (not pooled) based on both number of individuals and sampled coverage and then compared taxonomic and trait-based diversities only on sample coverage. Taxonomic and trait-based rarefaction and extrapolations have been done using the iNEXT (Hsieh et al., 2016) and iNEXT.3D (Chao, 2021) packages.

As functional diversity indices are sensitive to missing trait data (Májeková et al., 2016), specimens with any missing trait value were excluded from the analysis. A total of 939 individuals were excluded from the dataset (814 individuals we could not identify to morphospecies, including 200 adults, and 125 specimens for which at least 4 traits were missing). The analyses were performed using R (R Development Core Team, 2021).

Results

A total of 1613 spiders were sampled, among which a total of 572 (35%) were adults and 1011 (64%) were juveniles. 940 spiders were collected at the coastal sites, and 673 at the inland sites (see details in Table 1).

Table 1: Overall presentation of the sampled spider assemblages over the four sites of French Guiana (CSG= Centre Spatial Guyannais) and four forest types (SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg).

		Total nb	Juveniles		Adults		Family	MS	Singletons	Doubletons	Nb of
		of	Nb	%	Nb	%					
		individuals									with higher nb
											of individuals
CSG	SF	245	134	55%	109	44%	16	56	44	7	5
	TF	226	145	64%	80	35%	20	44	31	11	2
	WS	249	153	61%	95	38%	19	63	31	9	23
Laussat	SF	88	48	55%	36	41%	12	56	44	8	4
	TF	78	50	64%	27	35%	17	22	20	2	0
	WS	54	33	61%	21	39%	10	19	19	0	0
Nouragues	INS	31	19	61%	12	39%	13	5	2	3	0
	SF	117	66	56%	51	44%	18	22	17	4	1
Trinité	TF	204	152	75%	47	23%	20	22	19	1	2
	INS	49	38	78%	11	22%	14	9	7	2	0
	SF	141	88	62%	46	33%	20	36	32	2	2
	TF	131	85	65%	37	28%	19	28	27	1	0

Direct correlations between traits and between diversity metrics

Overall correlations between taxon- vs traits-diversities were high, whatever the metrics considered (yet the correlations tended to increase together from species richness to Shannon and Simpson diversities, Figures 1 and 2). We will consequently focus on describing patterns

of species richness for taxonomic diversity (TD) vs the four metrics of trait-based diversity (correlations between Shannon and trait-based diversity and Simpson and trait-based diversity will not be detailed in the text).

Single trait approach

Hunting guilds – The correlation between TD and FRic was moderate positive (Spearman correlation coefficient; $\rho = 0.45$, $P = 0.04$; Figure 1a). There was strong negative correlation between TD and FEve (Spearman correlation coefficient; $\rho = -0.91$, $P < 0.05$) and moderate negative correlation between TD and RaoQ (Spearman correlation coefficient; $\rho = -0.51$, $P = 0.01$).

Prosoma width – There was strong positive correlation between TD and FRic (Spearman correlation coefficient; $\rho = 0.67$, $P < 0.05$; Figure 1b). There was no significant correlation between TD and FEve (Spearman correlation coefficient; $\rho = -0.18$, $P = 0.43$) and RaoQ (Spearman correlation coefficient; $\rho = 0.40$, $P = 0.07$).

Tibia length – TD was strongly positively correlated to FRic (Spearman correlation coefficient; $\rho = 0.69$, $P < 0.05$; Figure 1c), and moderately to RaoQ (Spearman correlation coefficient; $\rho = 0.54$, $P < 0.05$). No significant correlation was found between TD and FEve (Spearman correlation coefficient; $\rho = -0.23$, $P = 0.31$).

Multi-trait approach

Hunting guilds and prosoma width – A moderate positive correlation was found between TD and FRic (Spearman correlation coefficient; $\rho = 0.59$, $P < 0.05$; Figure 2a). The correlation between TD and RaoQ was moderate negative (Spearman correlation coefficient; $\rho = -0.55$, $P < 0.05$). No significant correlation was found between TD and FEve (Spearman correlation coefficient; $\rho = 0.32$, $P = 0.15$) and FDiv (Spearman correlation coefficient; $\rho = -0.11$, $P = 0.64$).

Hunting guilds and tibia length – The correlation between TD and FDiv was moderate positive (Spearman correlation coefficient; $\rho = 0.50$, $P = 0.02$; Figure 2b). A strong negative correlation was found between TD and RaoQ (Spearman correlation coefficient; $\rho = -0.78$, $P < 0.05$). There was no significant correlation between TD and FRic (Spearman correlation coefficient; $\rho = 0.40$, $P = 0.07$) and FEve (Spearman correlation coefficient; $\rho = 0.39$, $P = 0.08$).

Prosoma width and tibia length – TD was strongly positively correlated to FRic (Spearman correlation coefficient; $\rho = 0.83$, $P < 0.05$; Figure 2c) and moderately correlated to RaoQ (Spearman correlation coefficient; $\rho = 0.55$, $P = 0.08$). There was not significant correlation

between TD and FEve (Spearman correlation coefficient; $\rho = 0.10$, $P = 0.65$) and FDiv (Spearman correlation coefficient; $\rho = -0.007$, $P = 0.97$).

Hunting guilds, prosoma width and tibia length – A moderate positive correlation was found between TD and FRic (Spearman correlation coefficient; $\rho = 0.54$, $P < 0.05$; Figure 3). The correlation between TD and RaoQ was very strong negative (Spearman correlation coefficient; $\rho = -0.82$, $P < 0.05$). No significant correlation was found between TD and FEve (Spearman correlation coefficient; $\rho = 0.25$, $P = 0.26$) and FDiv (Spearman correlation coefficient; $\rho = 0.08$, $P = 0.73$).

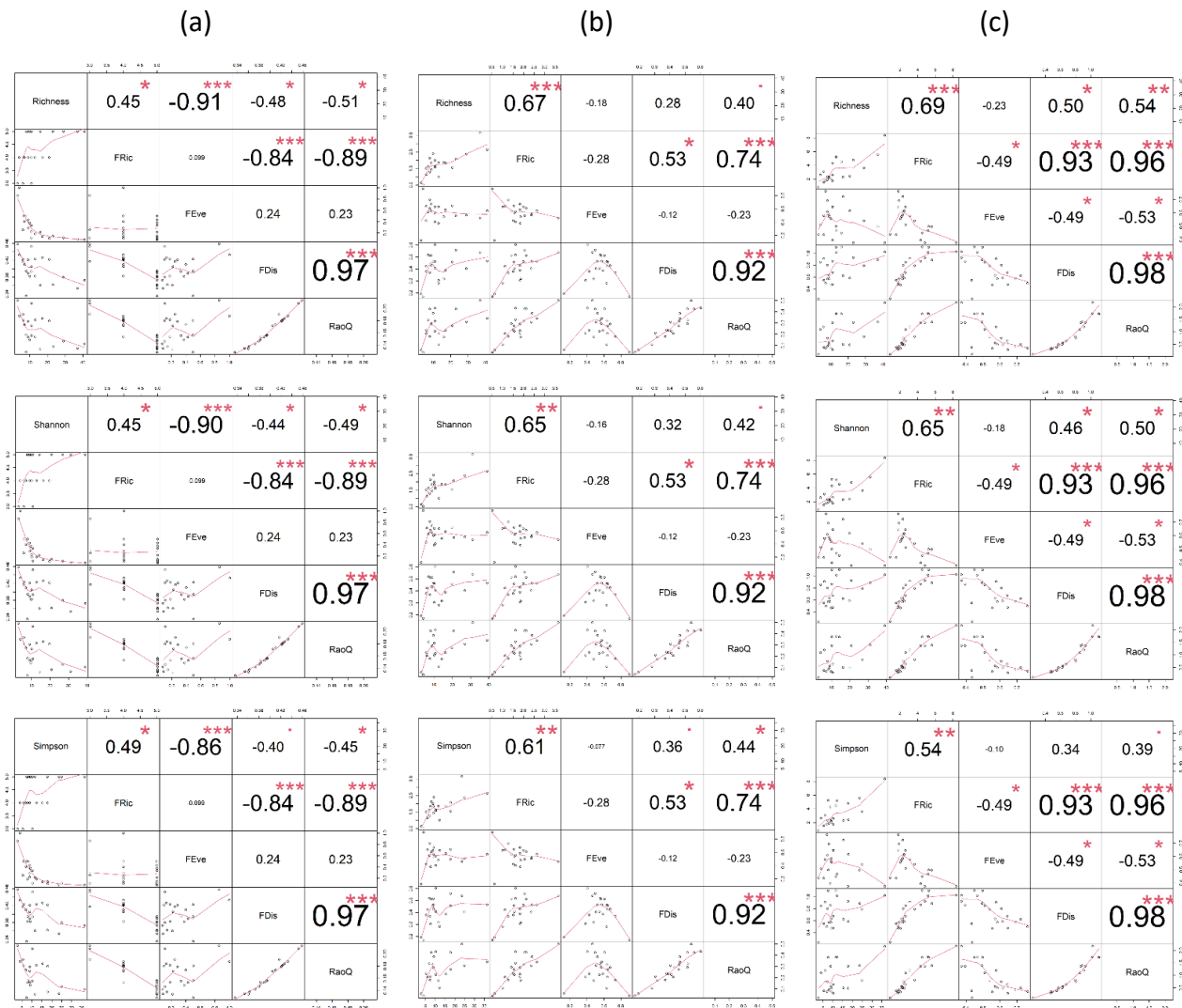


Figure 1: Correlations between TD (3 metrics) and trait diversity (4 metrics) depending on the trait considered for computing trait diversity (a: Hunting guilds, b: Prosoma width, c: Tibia length).

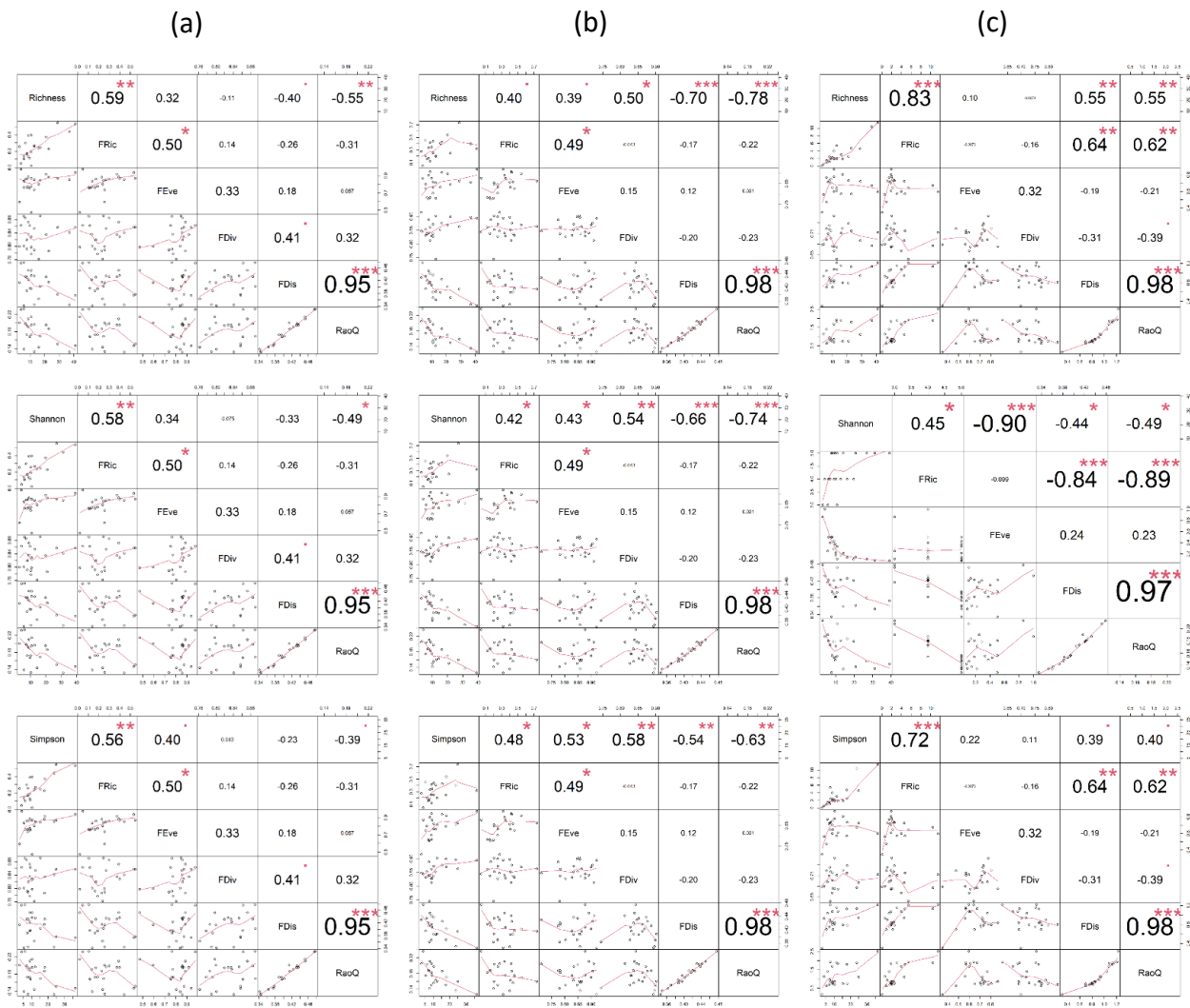


Figure 2: Correlations between TD (3 metrics) and trait diversity (4 metrics) depending on the combination trait considered for computing trait diversity (a: Hunting guilds and prosoma width, b: Hunting guilds and tibia length, c: Prosoma width and tibia length).

Comparison of patterns in taxonomic and trait-based diversity

Overall patterns of estimated taxonomic diversity were consistent between sites with similar environmental ranges (coastal vs. inland, Figure 4), with especially higher TD in WS forests vs SF forests and to a lesser extent compared to TF (coastal sites) and lower TD in Inselbergs forest as compared TD in TF and SF forests (the two latter were not significantly different in estimated TD, whatever q considered) (inland sites). Sites will consequently be mixed up in the subsequent results. Because of important variations of TD avoiding a proper comparison of the assemblages of the different habitats when estimations are based on the number of individuals, the subsequent comparisons of TD and trait-based diversity will be based on sample coverage.

Patterns of taxonomic diversity and influence of integrating juveniles

Whatever the metric considered and the stages integrated, forests on inselbergs had the lowest taxonomic diversity and forests on Terra Firme the highest (Figure 5). Integrating juveniles on top of adults did not influence TD patterns (see Figure 5a vs Figure 5c).

Patterns of trait-based diversity and influence of integrating juveniles

Whatever the metric considered and the stages integrated, forests on inselbergs had the lowest trait-based diversity and forests on Terra Firme the highest (Figure 6). Integrating juveniles on top of adults had little influence on trait-based diversity patterns (see Figure 6a vs Figure 6c).

Patterns of taxonomic vs. trait-based diversity

Patterns of taxonomic diversity vs trait-based diversity were finally very similar when compared for similar stages (see for adults: Figure 5a vs Figure 6a and for juveniles: Figure 5b vs. Figure 6b).

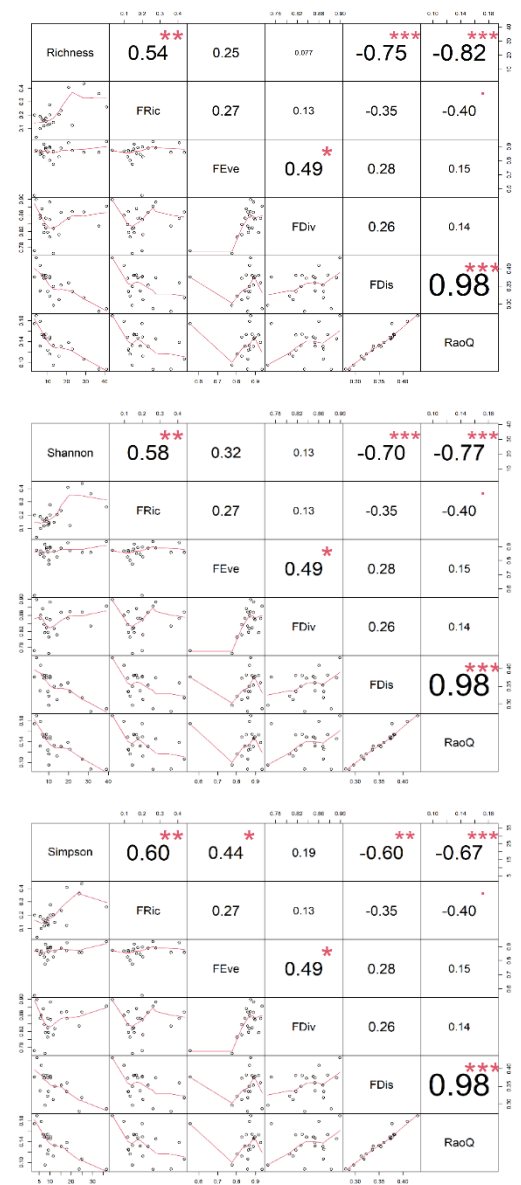


Figure 3: Correlations between TD (3 metrics) and trait diversity (4 metrics) for the combination of hunting guilds, prosoma width and tibia length.

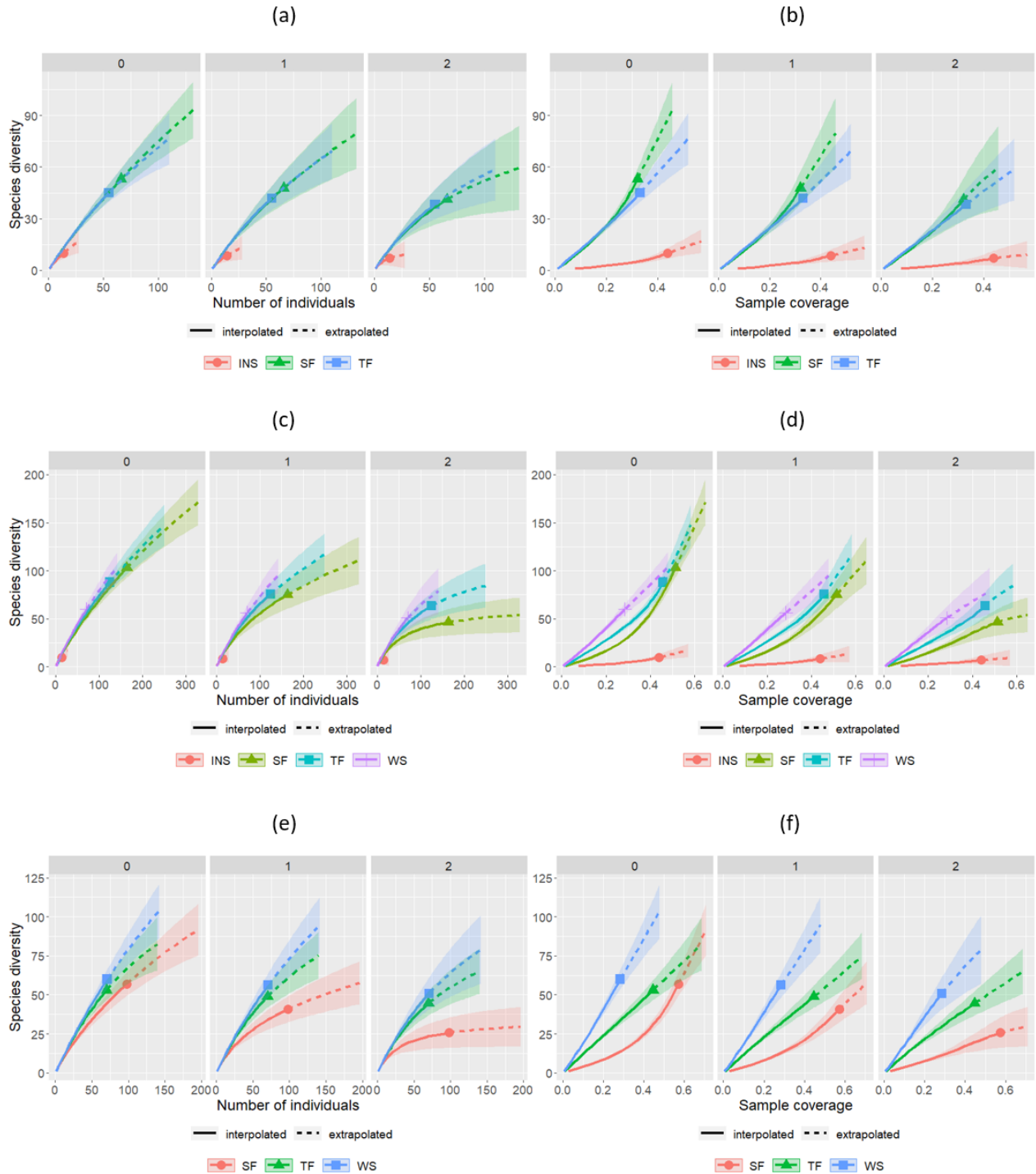


Figure 4: Estimated taxonomic diversity found between habitats based on number of individuals (left) or sample coverage (right) in coastal sites (a and b), inland sites (c and d), and all coastal and inland sites together (e and f). 0: taxonomic richness, 1: Shannon diversity, 2: Simpson diversity. Forest types: SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg.

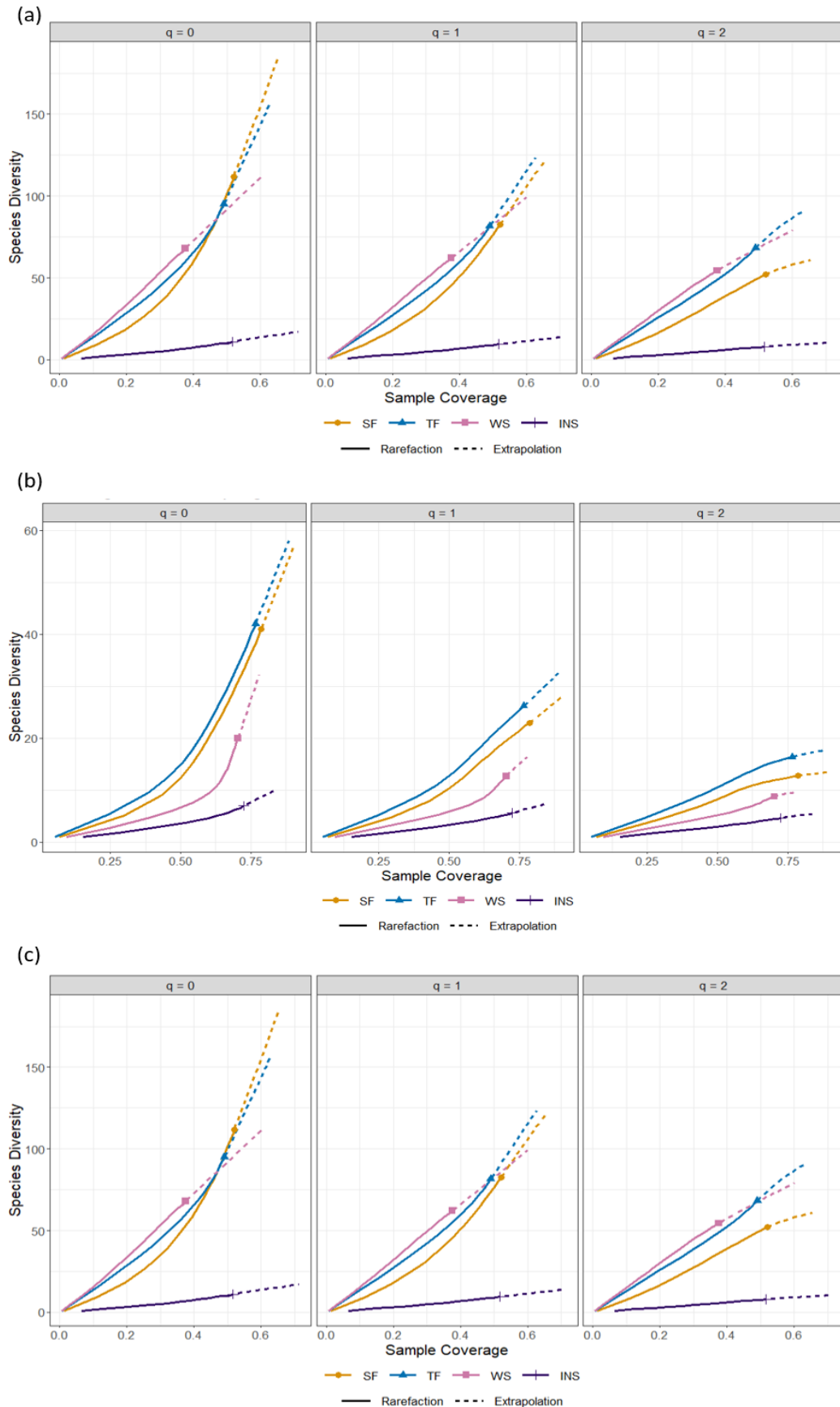


Figure 5: Estimated taxonomic diversity metrics in the 4 habitat types (SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg), considering adults only (a), juveniles only (b), or both (c).

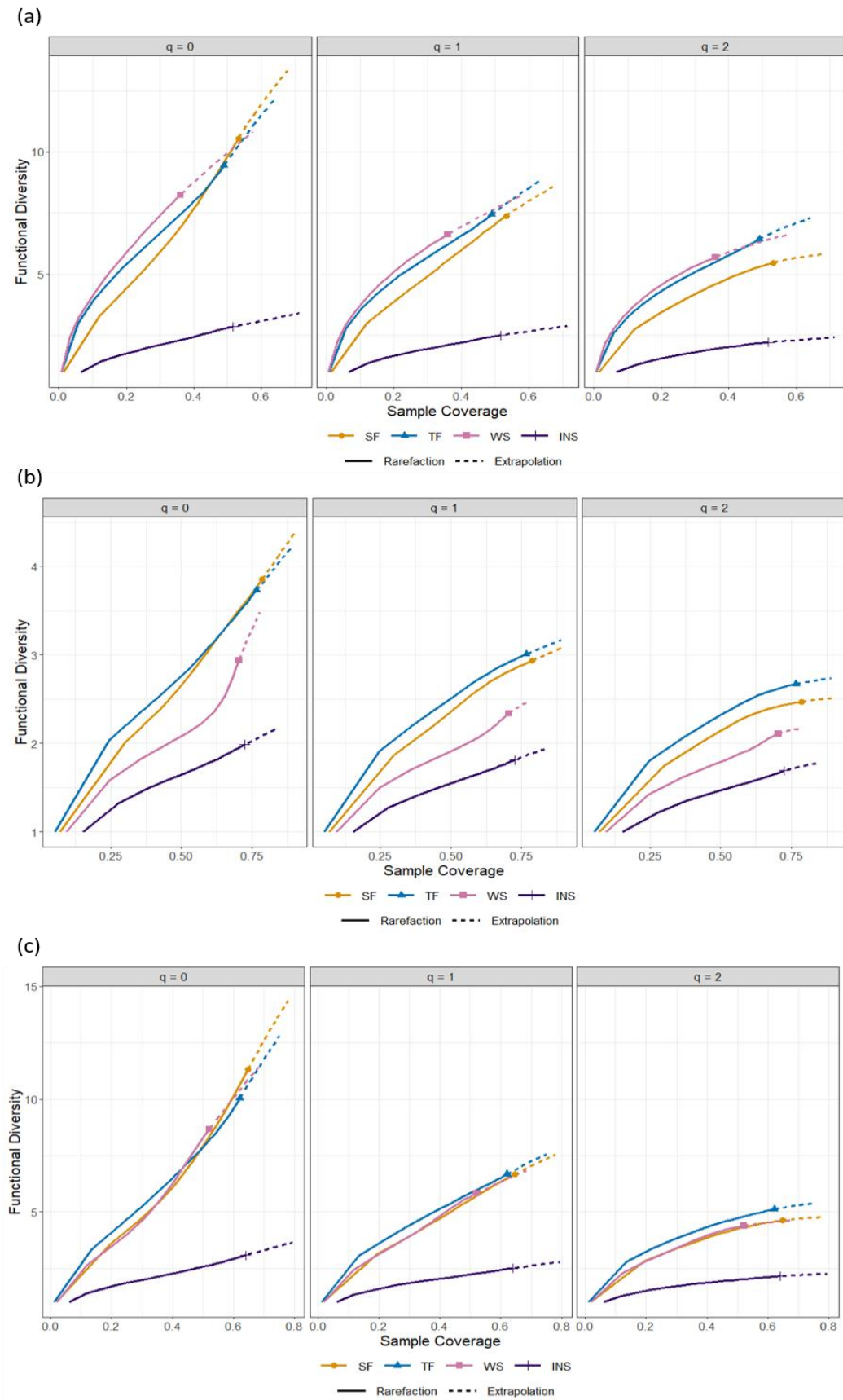


Figure 6 : Estimated trait diversity metrics in the 4 habitat types (SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg), considering adults only (a), juveniles only (b), or both (c).

Discussion

In this study, we investigated how taxon- and trait-based diversities vary across contrasted tropical forests habitats at broad geographical scales, and how several methodological impediments (number and nature of traits to be considered, integration of juveniles or not, q order) influenced the correlations of metrics (directly) and patterns (by comparison).

Overall taxon- and trait-based diversity metrics and patterns were highly correlated. Correlations between taxonomic and trait diversities are indeed supposed to increase with the level of environmental constraints (for plants: Cadotte et al., 2019), and one would therefore expect lowered correlations in tropical habitats (see also Privet & Pétillon, 2020 for spiders). Our results show a significant influence of forest type on both taxonomic and trait diversity patterns, probably revealing strong environmental filtering (see Ridet et al., 2021 for another example in, temperate, spiders; see also Fichaux et al., 2019 for an example on hyperdiverse taxa of arthropods in neotropical forests). The range of forests sampled in this study comprised contrasting soil, plant community structure and composition (Baraloto et al., 2007, 2011; Fine et al., 2010; Wittmann et al., 2011; Fortunel et al., 2014) driving differences in potential prey environments and shelters for arthropods (Price, 2002). A recent study, conducted in the same forests, has found that taxonomic and functional composition of arthropods assemblages (including Coleoptera, Lepidoptera, Hemiptera, Hymenoptera and Orthoptera but only a family of spiders) show a strong turnover among habitats (Lamarre et al., 2016). However, there are no differences in herbivory rate among these habitats (Lamarre et al., 2012) despite the plant defense theory (Janzen, 1974; Coley et al., 1985). The plant defense theory predicts fewer resources allocated in anti-herbivory defense in high-resource plant communities, such as terra firme and seasonally flooded forest, compared to low-resource plant communities, such as white sand forest and inselberg forests (Baraloto et al., 2013).

One potential explanation for the lack of differences in herbivory rate between the habitats may be the strength of the third trophic level, such as predators (spiders) and parasitoids, that regulates herbivore populations (Van Bael et al., 2003). This hypothesis, if proved, does not however explain the case of white sands forests which are low-resource plant communities with no different herbivory rate (Lamarre et al., 2012) but the lower abundances of arthropods (Lamarre et al., 2016) and intriguingly the highest taxonomic and functional diversities in spiders found in our study. White sand forests are characterized by specific vegetation (Medina et al., 1990; Fine et al., 2010) and unique assemblage of arthropods, including white-sand habitat specialists such as Delphacidae and Fulgoridae (Hemiptera), Lamarre et al., (2016), but are also located within the terra firme and seasonally flooded forests (Fine & Bruna, 2016). It would thus be interesting to investigate white sand forests spiders taxa composition and diet to see if they are similar to the one of the surrounding forests with the addition of spiders feeding preferentially on white-sand arthropods specialists.

Conversely, the lowest taxonomic and trait diversities were found on inselbergs, which is consistent with other studies on neotropical spiders (see e.g., Lalagüe et al. submitted and Privet et al., (2018)). Several factors were advocated to explain such a pattern, and these included harsh microclimatic conditions, thinner soil, and species-poorer vegetation (as compared with lowland conditions). The quite low taxonomic and functional diversity in seasonally flooded forests, especially visible when adults of spiders were considered (with juveniles or not), might finally be explained by the removal of litter and the absence of vegetation succession due to floods, which in turn affect spider assemblages, reducing both taxonomic and functional diversities (see e.g., Uetz, 1979 and Döbel et al., 1990, respectively).

Correlation between taxonomic and trait diversity is also expected to increase with the number of traits used (see for plants: Tucker et al., 2018). While several traits were highly correlated to each other, hunting guilds drove most of the trait diversity patterns (results not presented here but see Figure S1 in supplementary material), highlighting the importance of this trait in spider community ecology. Yet this trait needs to be carefully used because they might differ among species within one family (Dias et al., 2009) and probably within individuals of a given species (Suter & Benson, 2014). The trait composition of spiders assemblages will be determined and compared among the different habitats in the near future. Patterns of body size, if detected, could inform us on the size of the ecological niche of species (Novotný et al., 2006). Smaller species are expected in cooler environments, e.g., at high latitudes or altitudes (Entling et al. 2007), thus it could be that smaller individuals can be found on the inselbergs. Conversely, if no differences in body size are among habitats, that could be because the effects of elevation are lesser under tropical conditions (mainly because of a reduced temperature range: Overgaard et al., 2011). Another explanation could be that the effects of altitude on spider size (i.e., an increase in spider size: see e.g., Ameline et al., (2018)) might be balanced by soil succession and the resulting reduced prey availability (see Kounda-Kiki et al., 2004). Regarding other biometric traits we measured, longer legs were proved to increase speed on steep ground (Prenter et al., 2012), while proportionally shorter legs in flooded habitats were reported for one species of Ctenidae, some wandering spiders of tropical forests (Pétillon et al., 2018). Last, one should stress that size constraints on legs differ between web-building and cursorial spiders (Moya-Laraño et al., 2008). These hypotheses should be tested soon by looking at in-detail trait variations among habitat types.

While our results suggest important environmental filtering, even in tropical forests, the relative importance of deterministic vs neutral processes remains to be tested in the assembly rule of tropical forest spiders. Barcoding using several sequences could be used in complement to our current approaches to 1) challenge morphological segregation (see Courtial et al. in prep, Appendix 3 of the thesis) and be used to assess the phylogenetic diversity (see Dolson et al., 2020). The importance of juveniles could be then more important than what we observed when they are integrated into molecular approaches (Domènech et al., 2021). Environmental variables describing climate, soil and forest structure are available for these habitats (for complete details, see Baraloto et al., 2011). They were previously used in order

to define the environmental conditions of each studied plot (Lamarre et al., 2016) and will be used in the future to investigate the relationships between traits and environmental conditions as well as spider taxonomic and trait assemblages. The influence of species and traits in composition turn-over (patterns of β -diversity using Hill numbers) should also be investigated in the close future. Differences in environmental drivers are indeed expected between taxonomic and trait diversity, with complementary responses to abiotic gradients (see Wong et al., 2019 for a recent, general, review on arthropods). If the nestedness of beta taxonomic diversity is reported to increase when the number of species decreases (e.g., Hacala et al., 2020), this remains unexplored for beta trait (functional) diversity. Our study finally calls for better standardization of metrics, in terms of estimation methods and type of metrics (with a little influence of q order, except for increasing correlations between taxonomic and trait diversity metrics), but also for more actually-measured traits in arthropod community ecology.

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Supplementary Materials

Comparison of trait diversity with and without hunting guilds

Adults, juveniles and adults+juveniles trait diversity excluding hunting guilds, compared with the above plots including hunting guilds, reveal that hunting guilds is an influential traits (note the Y-scales are different, although patterns are generally similar).

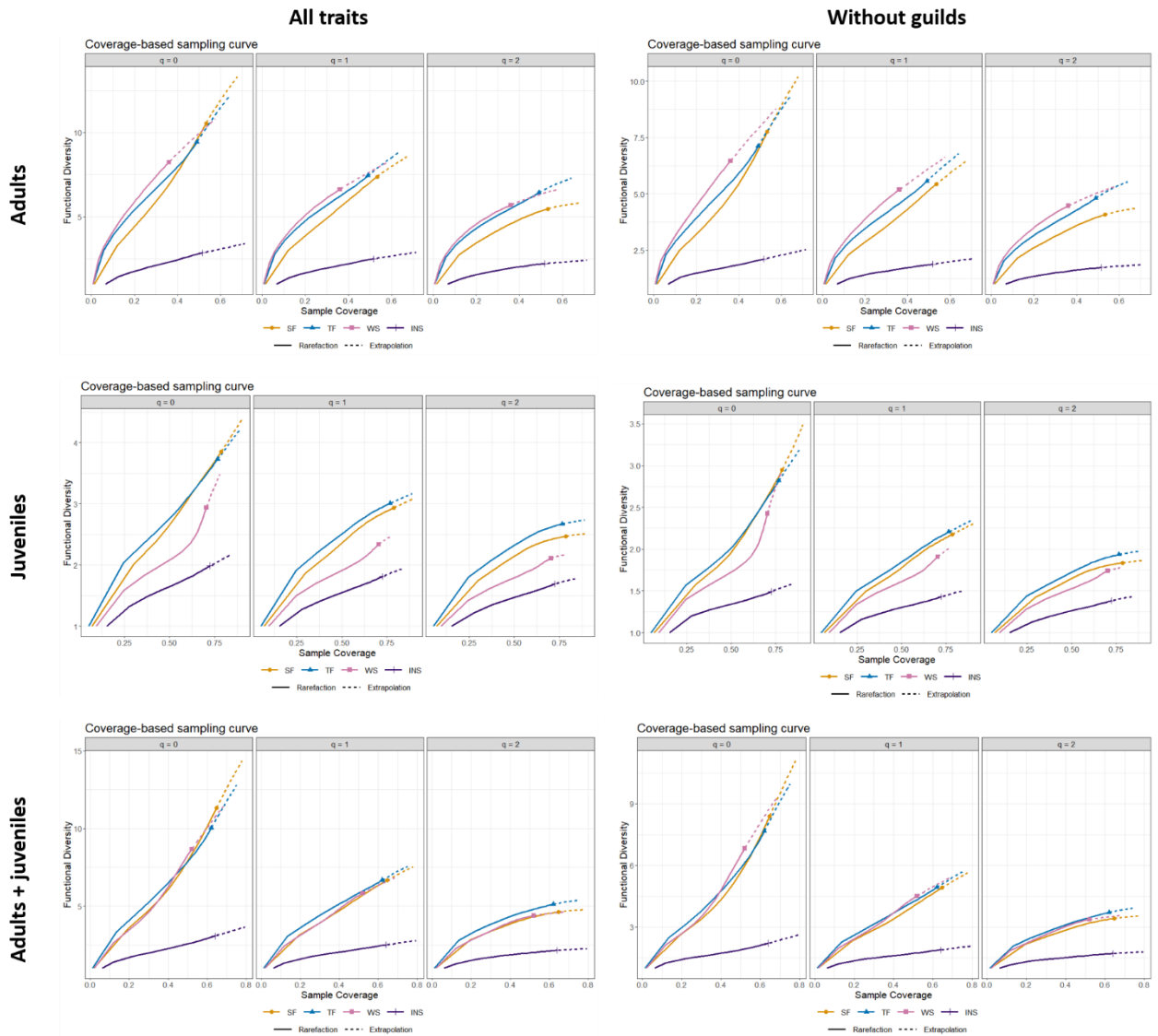


Figure S1: Patterns of trait diversities between habitats compared when all traits are taken into account (left column) and when hunting guilds are excluded (right column). Patterns for adults (first column), juveniles (second column) and both (third column) are shown.

PART III: DESCRIBING AND UNDERSTANDING TROPICAL SPIDER DIVERSITY USING A PHYLOGENETIC APPROACH: THE CASE OF HAWAIIAN WOLF SPIDERS

CHAPTER.5

Phylogenetic relationships among Hawaiian wolf spiders suggest recent radiation driven by the adaptation to different environments

Kaïna Privet, Henrik Krehenwinkel, Rosemary Gillespie and Julien Pétillon

This article is in preparation

Abstract

Understanding the origins of diversity patterns is a major challenge in ecology and adaptive radiation has been proposed as its main contributor. We used a system of wolf spiders distributed across different ecological conditions over islands of different ages in the Hawaiian archipelago to investigate patterns adaptation and speciation among taxa across islands and the role of habitat and altitude specialization. We developed a detailed, phylogenetic framework to determine boundaries and phylogenetic relationships between taxa. To do so we gathered the most complete collection of wolf spiders from the Hawaiian archipelago so far and investigated their phylogenetic relationships using a set of nuclear and mitochondrial markers and a high throughput sequencing approach to obtain data representative at multiple time-slices. The preliminary results show single-locus phylogenetic trees of low resolution with incongruences between loci. Despite this, these trees support lineages occurring on single or multiples islands. They also support an independent lineage of cave spiders including few surface relatives suggesting that adaptation to cave environment is evolutionarily labile. Among surface spiders, no congruent pattern of altitude-related speciation was found but further analyses are needed to better capture the role of altitude in Hawaiian wolf spider speciation.

Keywords: ecological divergence, Hawai'i, Lycosidae, cave, gene flow, phylogeography.

Introduction

Understanding the origins of diversity patterns is a major challenge in ecology. Current diversity is the product of ecological and evolutionary processes and their interactions. One process, **adaptive radiation**, has been proposed as the major contributor to global diversity (Simpson 1953, Schluter 2000). Adaptive radiation is the process by which organisms rapidly diversify from an ancestral species into a multitude of different new ecological forms (Gillespie *et al.* 2001). Adaptive radiation requires ecological differentiation coupled with reproductive isolation to allow speciation (Rundell & Price 2009). Adaptive radiation is thus acting at the intersection between ecology and evolution. Divergent natural selection arising from environmental or niche differences can lead to ecological divergence and speciation (called “ecological speciation”) and is thought to play a major role in driving adaptive radiation (Schluter 2000, Rundle & Nosil 2005, Nosil 2012). **Ecological speciation** has been well illustrated in many examples of recent adaptation of incipient species (e.g., Cichlid fishes and Asteraceae, respectively, Meier *et al.* 2018, Knope *et al.* 2020). However, the extent to which divergence into different habitats can lead to adaptive radiation is still unclear (Gillespie *et al.* 2020).

Islands, and in particular remote oceanic hotspot islands with a geological chronology, have been proposed as a system sufficiently simple to master at least some of the complexity, history, geography, and evolutionary adaptation required to untangle the origins of biodiversity in the context of adaptive radiation (Gillespie 2016). The **islands of Hawaii** are notably an unparalleled scientific laboratory for studying ecological and evolutionary processes at the origin of diversity due to their particular characteristics (Carson 1982, Baldwin & Sanderson 1998, Lerner *et al.* 2011, Brewer *et al.* 2015, Gillespie 2016, Gillespie *et al.* 2018). Indeed, the Hawaiian archipelago shows (i) extreme isolation, which results in the reproductive isolation of the colonists and can lead to speciation. Moreover, the Hawaiian archipelago consists of (ii) a series of islands that provides a replicated system for examining within-islands patterns of species formation across similar ranges of environmental extremes, and (iii) a chronological arrangement of the islands from Kauai (oldest) to Hawai’i (youngest) (Figure 1) that allows the examination of species formation within an identifiable chronological framework (Carson & Clague 1995). Finally, the Hawaiian archipelago also has (iv) a tremendous topographical range, a tropical position, a great range of climatic zones (Neall & Trewick 2008), and consequent environmental diversity that provides a huge ecological spectrum for species differentiation. Due to their age, the older islands of the Hawaiian archipelago have undergone erosion. However, the youngest island of Hawaii, is currently located over the hot spot and still has active volcanoes (the last eruption started on September 29, 2021), making the Hawaiian archipelago the group of islands that reaches the greatest altitude with the twin peaks of Mauna Kea volcano at 4207 m and Mauna Loa volcano at 4169 m (Figure 2).

Spiders are particularly suitable organisms to study patterns of diversification at the intersection between ecology and evolution because their ecology is readily apparent through their very tight habitat affinities (Foelix 2010) and their observable hunting behaviors. On the islands of Hawaii, the **wolf spiders (Lycosidae)** are found from low to high elevations, on coastal sites, wet forests, lava flows, summit deserts, and likewise in lava caves (Keyserling 1890, Simon 1900, Gertsch 1973, Howarth 1983, 1987b, Duman & Montgomery 1991). Therefore, they are one of the spider families whose ecological range includes the most contrasting physical environments in the Hawaiian archipelago (Howarth & Montgomery, 1980). Across these well-defined habitats, Hawaiian wolf spiders show marked morphological and lifestyle differences: there are web-spinning wolf spiders in forests (Simon 1900) and ground-dwelling wolf spiders on surface lava flows (Howarth & Montgomery 1980). In lava caves, wolf spiders show reduction or loss of eyes and body pigments (Howarth 1972, Gertsch 1973), along with other attributes to subterranean existence, including low reproductive rates, a reduced number of offspring, and long periods to maturity (Hadley *et al.* 1981, Howarth 1993). These differences suggest the possibility that Hawaiian wolf spiders differentiated across habitats unlike most other endemic spider taxa in Hawaii that have largely diversified within the same environment (wet forest) (Hiller *et al.* 2019), such as *Tetragnatha* (Tetragnathidae)

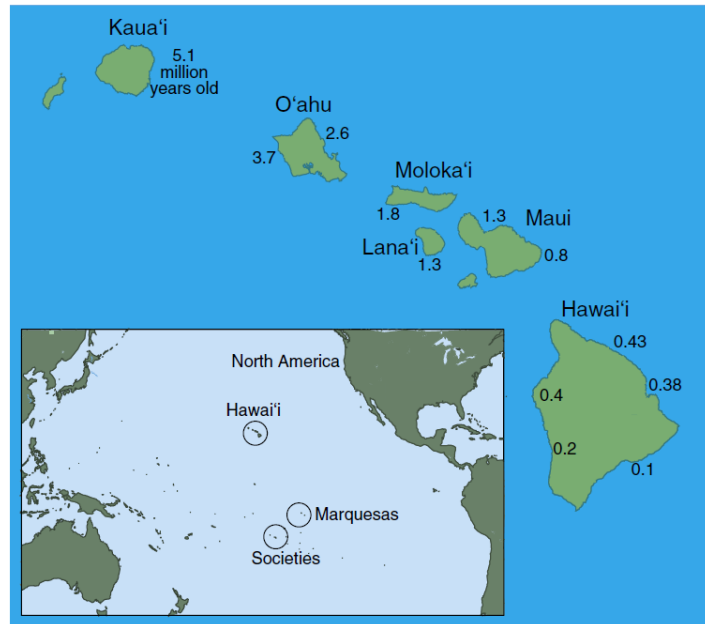


Figure 7: The Hawaiian archipelago chronosequence. The numbers indicate volcano geological ages, in millions of years. The still-growing island of Hawaii'i is the youngest (reproduced from Gillespie, 2005).

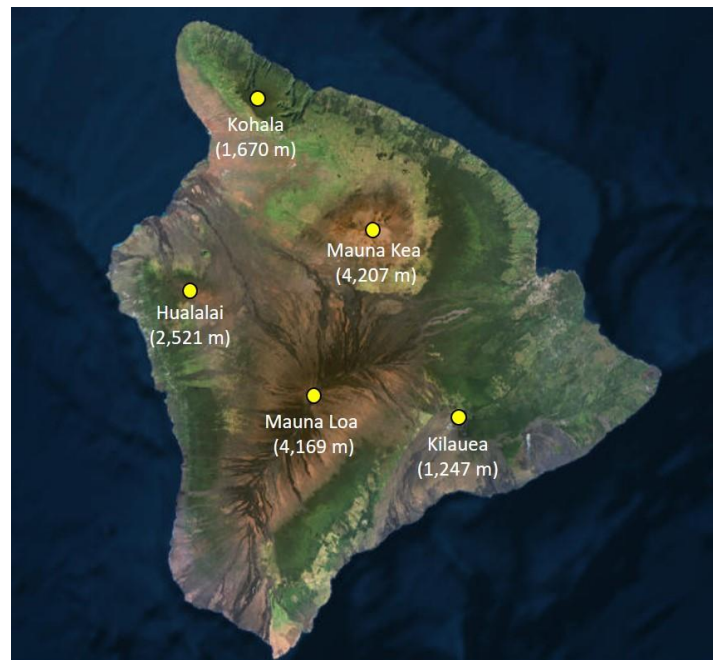


Figure 8: Map of the island of Hawaii mentioning the five volcanoes and their elevation.

(Blackledge & Gillespie 2004, Blackledge *et al.* 2009), *Ariamnes* (Theridiidae) (Gillespie *et al.* 2018), *Mecaphesa* (Thomisidae) (Garb & Gillespie 2009) and *Havaïka* (Salticidae) (Arnedo & Gillespie 2006).

This study aims to address the hypothesis that population divergence and species formation in Hawaiian Lycosidae are associated with adaptation to different environments in allopatry.

In the Hawaiian Islands, 18 species of wolf spiders in 11 genera (see the list in Table 1) (Suman 1964, Gillespie *et al.* 1998, Nishida 2000) are currently named. Among those, 11 are thought to be endemic (Suman 1964, see Table 1). The endemic species belong to two subfamilies and seven genera: Lycosinae (*Hogna*, *Trochosa*, *Alopecosa*, *Adelocosa*, *Lycosa*) and Artoriinae (*Lycosella*, *Syroloma*). The Lycosinae subfamily has a worldwide distribution while Artoriinae is known from Australasian, Oriental, Pacific regions (Framenau 2007) and South America (Piacentini & Ramírez 2019). In the Hawaiian Islands, the Lycosinae subfamily are ground-, lava-, and cave-dwelling spiders, while Artoriinae are vegetation web-spinning spiders. These two subfamilies suggest that there have been at least two colonization events and sources at the origin of the Hawaiian wolf spider fauna.

However, assignments to genus and species may have little validity for these Hawaiian wolf spiders. Wolf spiders represent relatively recent radiation of arachnids (Jocqué & Alderweireldt 2005, Garrison *et al.* 2016, Wheeler *et al.* 2017) with a strong morphological conservatism which has caused enormous confusion in their systematics (e.g., paraphyletic and polyphyletic genera) due to the lack of useful characters to define and separate genera and species (Vink *et al.* 2002, Jocqué & Alderweireldt 2005). Their morphological conservatism seems even more prominent on the Hawaiian archipelago, and we are lacking characters to separate species (Framenau, pers. comm.; Pétilon, pers. comm.). Within the Lycosinae subfamily, it has been suggested that all species belong to the genus *Hogna* and they are more species than what is currently described (Framenau, pers. comm.). Thus, **the current species designations are questionable**, but no taxonomic revision has been performed to date. Moreover, **knowledge about the described species is limited** as we have incomplete information on the natural history and the distribution of the described species. **Consequently, the genetic approach seems essential to better describe and understand their diversity and its origin.**

Using this system of wolf spiders distributed across different environments over islands of different ages in the Hawaiian archipelago, we developed a detailed, phylogenetic framework to **determine species boundaries and phylogenetic relationships between taxa**. We aim at answering the questions developed hereafter.

Table 1: List of the named wolf spider species from the Hawaiian archipelago known to date. Distributions are given according to the World Spider Catalog (2021), species descriptions, Hawaiian checklist (Nishida 2000), and arachnologist databases (Volker Framenau, pers. comm.). See Figure S1 for a map of the distribution of the endemic species in the current state of knowledge.

Subfamily	Genera	Species	Distributions	Status in Hawaii
Lycosinae	Adelocosa	<i>Adelocosa anops</i> Gertsch, 1973	Hawaii (Kauai is.)	Endemic
	Alopecosa	<i>Alopecosa oahuensis</i> (Keyserling, 1890)	Hawaii (Oahu and Hawaii is.)	Endemic
	Arctosa	<i>Arctosa aliusmodi</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
	Hogna	<i>Hogna bruta</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
		<i>Hogna crispipes</i> (L. Koch, 1877)	Australia (mainland, Norfolk Is.), New Guinea, Vanuatu, Polynesia, New	Introduced (all islands)
		<i>Hogna hawaiiensis</i> (Simon, 1899)	Hawaii (Oahu, Maui and Hawaii is.)	Endemic
	Lycosa	<i>Hogna likelikeae</i> (Simon, 1900)	Hawaii (Kauai is.)	Endemic
		<i>Lycosa howarthi</i> Gertsch, 1973	Hawaii (Hawaii is.)	Endemic
		<i>Lycosa perkinsi</i> Simon, 1904	Hawaii (Oahu is.)	Endemic
	Schizocosa	<i>Schizocosa vulpecula</i> (L. Koch, 1865)	Wallis is.	Introduced (Maui is., Oahu is.)
	Trochosa	<i>Trochosa kalukanai</i> (Simon, 1900)	Hawaii (Kauai is.)	Endemic
	Vesubia	<i>Vesubia caduca</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
Artoriinae	Anoteropsis	<i>Anoteropsis virgata</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
	Lycosella	<i>Lycosella annulata</i> Simon, 1900	Hawaii (Oahu is.)	Endemic
		<i>Lycosella spinipes</i> Simon, 1900	Hawaii (Kauai and Hawaii is.)	Endemic
	Syroloma	<i>Syroloma major</i> Simon, 1900	Hawaii (Kauai, Oahu, Maui and Hawaii is.)	Endemic
		<i>Syroloma minor</i> Simon, 1900	Hawaii (Kauai, Molokai, Maui and Hawaii is.)	Endemic

Question 1: what are the phylogenetic relationships between wolf spiders found on different islands?

Based on preliminary data, it appears that: (i) members of the subfamily Lycosinae are likely all within the genus *Hogna*, and are morphologically conserve at the surface, (ii) members of the

subfamily occurs at different elevations at the surface of all the main islands, and down to caves on two islands, we suggest that:

Hypotheses: Hawaiian wolf spiders “morphological conservatism” might reflect the absence of differentiation of surface spiders, related to a recent radiation or gene flow occurring between diverging lineages found on different islands and among islands on different elevations.

Question 2: What are the phylogenetic relationships between surface spiders found at different elevations? Is there an altitudinal pattern of phylogenetic relationships? The case of the island of Hawaii

The surface members of the Lycosinae (in contrast to those in caves) are found from low to high elevations. Investigations conducted prior to this thesis, by Julien Pétillon (unpublished), on wolf spiders found all along the slope of the Mauna Kea volcano (above 1000m to the summit) from the island of Hawaii (Figure 2), concluded that these wolf spiders seem morphologically very similar although showing confusing genitalic diversity for a single species. It was thus not possible to determine if they were different species or populations of the same species. These wolf spiders encounter very different living conditions. The wolf spiders found at the summit of the Mauna Kea volcano (>4000 m) live in an alpine stone desert covered by snow for part of the year (high altitude aeolian system) (Howarth & Montgomery 1980, Englund *et al.* 1999). This alpine desert consists mainly of a mix of unvegetated lava rock and semi-vegetated lava flows, covered by alpine tundra (Hawaiian tropical high shrublands). The precipitation is low and the temperatures are extremes with warm days and cold nights (Howarth 1987b). The wolf spiders hide in cracks and under rocks during the day and only venture onto the surface at night or when suitable prey appears (Howarth 1987b). Duman & Montgomery (1991) highlighted that one of these species (referred to as *Lycosa sp.*) is not freeze tolerant but survives by avoiding low temperatures through high mobility to quickly move into thermally buffered microhabitats. Other wolf spiders found along the slope of the volcano live on lava flows, one of the most inhospitable environments on earth (neogeoaeolian system, Howarth 1979). There the daily surface temperature fluctuations often approach 50°C and the rain either percolates into the porous rock or evaporates to render it very xeric (Howarth 1987b). These lava flow are from different ages, and left intact some “islands” of vegetation are called “kipuka”, from which wolf spiders are surprisingly absent (Vandergast & Gillespie 2004, Pétillon *et al.* 2020).

Hypotheses: consequently, we suggest that the living conditions on these ecosystems are harsh and differ between summit (Aeolian system) and slope (Neogeoaeolian system). Therefore, there could be two ecotypes (species adapted to specific environmental conditions): the first living in the alpine desert of the summit, the second living on lava flows on the slope of the volcano.

Question 3: What are the relationships among cave wolf spiders and between cave- and surface wolf spiders?

Among the endemic wolf spiders of the islands of Hawaii, two species (*Adelocosa anops* and *Lycosa howarthi*) are troglobitic and have adapted to cave life through eye and pigment modification, as well as physiological changes (Hadley *et al.* 1981). With another species found in French Polynesia (*Nukuhiva adamsoni*) (Framenau & Lehtinen 2015), these are the only known representatives of cave adaptation in wolf spiders globally (Mammola & Isaia 2017). A first species, *Adelocosa anops* Gertsch, 1973, is found on the oldest high island (Kauai) and has undergone a complete loss of eyes (Gertsch 1973) (Figure 3). A second species, *Lycosa howarthi* Gertsch, 1973, is found on the youngest island (Hawaii) and has only undergone a reduction of its eyes (Figure 3) (Gertsch 1973, Hadley *et al.* 1981, Howarth 1987a). This species is found in cave systems of different ages (Table 3).

Hypotheses: Considering that the islands of Kauai and Hawaii have never been connected, we suggest that the two troglobitic species have evolved independently from surface relatives. We test the hypothesis considering that the difference in eye loss and islands between these two species could be related to (1) independent colonization of caves from surface relatives (*L. likelikeae* on Kauai; *H. hawaiiensis* on the island of Hawaii), and (2) the older age of Kauai (5 my) compared to Hawaii (0.5 my), resulting in a longer time to adapt to cave life (Howarth 1993, Framenau & Lehtinen 2015). On the island of Hawaii, *L. howarthi* is found in cave systems that are of different ages. We thus suggest that the species colonized the caves multiple times, allowing the assessment of divergence replicated on the same landscape but at different times.

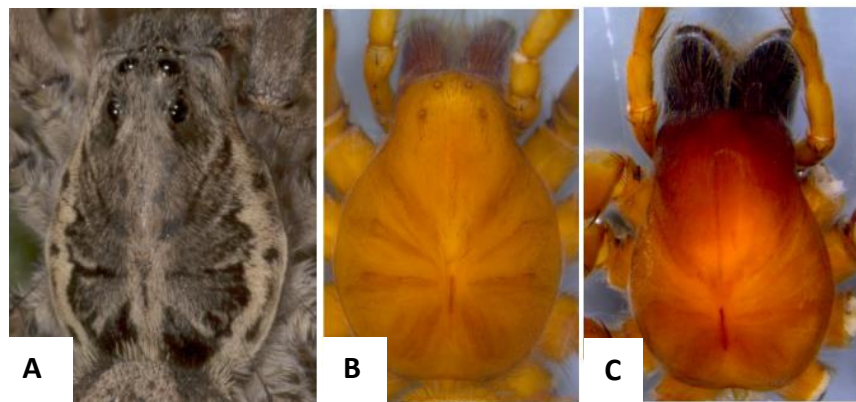


Figure 3: A: surface-dwelling Hawaiian wolf spider (*Hogna crispipes*); B: cave-dwelling wolf spider with reduced eyes (*Lycosa howarthi*) only known from the youngest island of the archipelago (Hawaii); C: cave-dwelling wolf spider with no eyes (*Adelocosa anops*) known from the oldest island of the archipelago (Kauai). (Images from Framenau and Lehtinen, 2015).

We tested these hypotheses by collecting spiders from the main islands of the archipelago, from cave and surface. We then studied their phylogenetic relationships using a set of nuclear and mitochondrial markers and high throughput sequencing approach to obtain data representative at multiple time-slices within the phylogeny. We present here preliminary results obtained on their phylogeny.

Materials and methods

Taxonomic sampling

For this study, we gathered a total of 217 Lycosinae spiders from 9 islands (see Tables 2 and 3 for details on the collected samples and the caves but see Table S1 in supplementary data for a complete list). Some of these samples were from field trips conducted on the islands of Molokai and Hawaii between 2016 and 2017. These specimens were kept in 96% or 100% ethanol at -20°C before extraction. Other field expeditions were planned during this Ph.D. to complete the sampling for most of the main Hawaiian Islands but were canceled due to the Covid-19 pandemic. The other part is museum specimens, mostly not identified to species, that were collected from 1931 to 2017 and provided by the Bernice Pauahi Bishop Museum (Honolulu, USA), Muséum National d'Histoire Naturelle (Paris, France), the Queensland Museum (Queensland, Australia), the Essig Museum of Entomology (Berkeley, USA), the Musée des Confluences (Lyon, France) and personal collections (Rosemary Gillespie, Jesse Eiben, Megan Porter, Natalie Graham). Most of these specimens were kept in 70% ethanol at room temperature since their collection.

Spiders identified as *Hogna crispipes* (introduced) are included to ascertain their phylogenetic assignments, as well as spiders belonging to the other subfamily known from the Hawaiian Islands, Artoriinae. The originally described species of Artoriinae have not been recorded during our field trips and we consequently used Museum material. Moreover, we included specimens of *Hogna radiata*, the European type species of the genus *Hogna* to test the taxonomic placement of Hawaiian *Hogna*, and a specimen of *Bradystichus crispatus* (Pisauridae) as the outgroup.

Table 2: Origin of the wolf spiders studied according to the island, volcanoes, and elevations they were collected in. Information about the date of collection is given.

	Islands (from oldest to youngest)	Number of specimens		Volcanoes/elevation (maximum elevation on the island)	Date of collection	
Northwestern Hawaiian islands	Laysan	3		-	1959-1987	
	Necker	2		-	1982	
	Nihoa	2		0m	2015-2016	
Main Hawaiian islands	Kauai	20 including	16	Up to 1158m (max 1598m)	1963-2016	
			4	Caves – Koloa caves (3), Kiahuna (1)	1971-1979	
	Oahu	15		Up to 700m (max 1220m)	1933-2015	
	Molokai	21		0-300m (max 1512m)	2016	
	Lanai	1		457m (max 1026m)	1973	
	Maui	20		0-3000m (max 3055m)	1975-2016	
	Hawai'i	133 including	1		Hualalai volcano – 1310 m (max 2521m)	1972
			55		Mauna Kea volcano – up to 4168 (max 4207m)	1992-2018
			30		Mauna Loa volcano – up to 4053m (max 4169m)	1971-2016
27				Kilauea volcano – up to 1247m (max 1247m)	1971-2016	
		20		Caves – Kaumana cave system (1), Happy hobbit cave system (1), Kipuka Kanohina cave system (18)	No date, 2016, 2018	

Table 2: Island, volcano, age and altitudes of the sampled caves.

Island	Volcano	Cave system	Cave (section)	Age* in years	Elevation in m**	
Kauai		Koloa Cave 2	Kiahuna	150,000-500,000	0	
Hawai'i	Mauna Loa	Kaumana	Kaumana cave	140 (1881 flow)	300	
		Keokeo	Happy Hobbit	1,500-3,000	550-750	
	Kīlauea	-	Ainahou cave	550-600 (Aila'au Flow)	920	
	Kīlauea	Kazamura	Kazumura cave	550-600 (Aila'au Flow)	410	
	Mauna Loa	Kipuka Kanohina	Kula kai		1,500-3,000	900
			Akea ka Mai		750-1,500	200-450
			Cordwinder Cave		750-1,500	200-450
			Eli's Cave		750-1,500	200-450
			Maelstrom		750-1,500	200-450
			Sea reef		200-1,000	1,150-1,400
		Xanadu		750-1,500	100	

* lave flows, according to Barton & Charlesworth 1984, Templeton 2008, Bosted *et al.* 2013, Aue 2014)
 ** at cave entrance, rounded

Selection of molecular markers of interest

Choosing markers to study the Hawaiian wolf spider radiation was a compromise of several criteria including (1) the need to study multiple time-scales to unravel the diversification and colonization patterns, (2) the fact that most of the samples are museum samples with degraded DNA, (3) the relatively recent age of the family, (4) the absence of a broad-scale phylogeny of the family, (5) the presence of paralogous copies of nuclear genes (Murphy *et al.* 2006) and (6) the mitonuclear discordance in wolf spiders (Vink & Paterson 2003, Ivanov *et al.* 2018, 2021) and (7) the broader objectives of the study the wolf spider radiation at the scale of the Pacific, including the already known phylogeny of the Galapagos wolf spiders.

Wolf spider phylogenetic studies have recently shifted from single locus (e.g., Zehethofer & Sturmbauer, 1998; Vink *et al.*, 2002) to multilocus studies using the genes 12S, NADH, 28S and COI (Murphy *et al.* 2006, Planas *et al.* 2013, De Busschere *et al.* 2015, Piacentini & Ramírez 2019). The use of genomic-scale approaches has just started in systematic studies (Ivanov *et al.* 2018, 2021).

12S and NADH1 are genes known to be useful to resolve relationships between closely related genera but are too conservative for adequate resolution at species level (Zehethofer & Sturmbauer 1998, Hedin & Maddison 2001, Vink *et al.* 2002, Vink & Mitchell 2002). 28S is also

known to resolve deep relationships, e.g., at the family level (Vink *et al.* 2002) but recent molecular attempts found that Lycosidae contains paralogous copies of the 28S, making it unsuitable for phylogenetic analysis (Murphy *et al.* 2006). By contrast, COI is a widely used gene that usually performs well in taxonomic assignments, be it between closely related species, genera, or subfamilies. However, COI trees have been observed to conflicted conspicuously with trees computed from other genes or parts of the mitochondrion (NADH1, 16S, 28S) (Vink & Paterson 2003). Moreover, and while nuclear protein-coding genes like Actin 5C and Histone 3 have not been extensively used in wolf spider phylogenetic analyses, they have proven to be useful in resolving the radiation of the Galapagos wolf spiders (De Busschere *et al.* 2012, 2015).

Recently, Krehenwinkel *et al.* (2018) developed a set of primers and a simple multiplex PCR protocol for arthropod systematic and phylogeny by Illumina amplicon sequencing. Their primers were established as effective phylogenetic markers for spiders in general (Kennedy 2018, Krehenwinkel *et al.* 2018) and were used in this study (Table 4).

DNA extractions

The amount of material collected from specimens varies from one leg to the entire spider (juveniles), according to the size of the specimen. For small adult specimens, genitalia were removed and kept as a voucher. Specimens were dried on absorbent paper, the selected parts were cut off using sterile razor blades and put into a new 1.5 mL tube. Samples were weighed and then placed at -20°C until extraction. DNA was extracted using DNEasy Blood and Tissue kit (Qiagen) or Puregene Gentra kit (Qiagen). Extractions using DNEasy Blood and Tissue kit were done following the manufacturer's protocol slightly modified. Notably, samples were incubated for three hours at 56°C, the volume of ATL Buffer, proteinase K, Buffer AL, and Ethanol 100% were increased accordingly to the size of the specimen, two elutions in 50µL were realized in separate tubes, columns were incubated at 65°C for 3 min before the final centrifugation step, which was modified to 2 min at 9,000 rpm. When using Puregene Gentra kit, samples were frozen in liquid nitrogen and grind using micropestle before following the manufacturer's protocol slightly modified. Notably, samples were incubated at 55°C overnight (at least 15 hours) with Proteinase K, and 0.5µL of Glycogen was added to increase DNA precipitation. All museum samples were extracted using Puregene Gentra kit (Qiagen), in the same laboratory facilities as recent specimens but their extractions took place months later to ensure that there were no recent DNA remnants. Moreover, extraction sessions were spaced in time to reduce cross-contamination pressure. The small amount of material and the poor state of conservation of most of the museum specimens did not allow the extraction to be replicated. DNA concentrations and quality were assessed using a Nanodrop spectrophotometer and agarose gels, respectively.

Table 3: Targeted loci, primer combinations, primer sequences including Illumina sequencing tails, expected length and average amplicon length. The “*” close to the ID indicates the loci for which we interpreted the phylogenetic trees.

Region	Locus	ID	Primers	Sequence 5'-3'	Length (bp)	Average amplicon length	
Mitochondrial	COI	COI	mICOLintF	ACACTCTTCCCTACACGACGCTCTCCGATCTGGWACWGGWTGAACWGTWTAYCCYCC	365	318	
			Fol-degen-rev	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTTANACYCNGGRTGNCCRAARAAYCA			
	CytB	CytB	CB3C	ACACTCTTCCCTACACGACGCTCTCCGATCTGAGGDGCHACHGTWATNACNAA	401	-	
			CB4A	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTRAARTATCATTCDGGTTGNATNTG			
	12SrDNA	12S	*	12SF1	ACACTCTTCCCTACACGACGCTCTCCGATCTNCHACTWTGTTACGACTT	424	400
			12SR1	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTAMTAGGATTAGATACCCT			
	16SrDNA	16S	*	16SF2	ACACTCTTCCCTACACGACGCTCTCCGATCTAATYCAACATCGAGGTCGCAA	371	315
			16SR2	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTTRACYGTRCWAAGGTAGCAT			
	18SrDNA	18S_A	*	SSU_F04	ACACTCTTCCCTACACGACGCTCTCCGATCTGCTTGCTCTCAAAGATTAAGCC	421	371
			SSU_R22	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTGCCTGCTGCCTTCCTTGGA			
18SrDNA	18S_B	*	18s_2F	ACACTCTTCCCTACACGACGCTCTCCGATCTAACTAAAGRAATTGACGGA	351	272	
		18s_4R	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTCKRAGGGCATYACWGACCTGTTAT				
Nuclear	28SrDNA	28S	*	28s_3F	ACACTCTTCCCTACACGACGCTCTCCGATCTTTTTGGTAAGCAGAACTGGYG	363	314
			28s_4R	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTABTYGCTACTRCCACYRAGATC			
	ITS2	ITS2	*	5.8S3F	ACACTCTTCCCTACACGACGCTCTCCGATCTATCACTHGGCTCRYGGRTCGATG	436	435
			28S2R	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTTCTTTCTCCSCTHANTDATATGC			
Histone H3	H3		H3aF	ACACTCTTCCCTACACGACGCTCTCCGATCTATGGCTCGTACCAAGCAGACVGC	374	328	
			H3aR	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTATATCCTTRGGCATRATRGTGAC			
Actin 5	Act5		Actin2_F2	ACACTCTTCCCTACACGACGCTCTCCGATCTGAYTTYGARCARGARATGGCNAC	270	226	
			Actin2_R1	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTGRTCDGCAATNCCWGGRTACAT			

PCR amplifications

PCR was used to amplify a total of nine markers (summarized in Table 4), of which one was protein-coding mitochondrial markers (Cytochrome B (Cyt B) and Cytochrome Oxidase I (COI)), two protein-coding nuclear markers (Actin 5 (Act5) and Histone H3 (H3)), two non-coding ribosomal mitochondrial markers (12S and 16S), and three non-coding ribosomal nuclear markers (18S, 28S and ITS2). PCR primers contained 5'-tails from Illumina to perform a subsequent indexing PCR.

DNA samples were standardized to 10 ng/μL except those whose initial concentration was lower than 100 ng/μL (estimated by Nanodrop), which were not diluted. Recovery of the primers was tested primer per primer and in two multiplex PCR, one grouping the mitochondrial primers (COI 12S and 16S) and another the nuclear primers (Act5, H3, 18S, 28S, ITS2). PCR tests were conducted on a subset of samples using the Multiplex PCR kit (Qiagen) following the manufacturer's protocol and Krehenwinkel *et al.* (2018) annealing temperatures: initial denaturation of 15 min at 95°C; 25 cycles of: a denaturation step of 30 sec at 94°C, an annealing step of 1min 30 sec at 46°C for mitochondrial genes and 55°C for nuclear genes, an extension step of 1 min 30 sec at 72°C; and a final extension of 10 min at 72°C. PCRs were run in 15μL containing 1X of Qiagen Multiplex Master Mix, 0.2μM of each primer and 1.5μL of DNA (0.2 to 10 ng/μL final). Amplification control was done using agaroses gel. Amplifications were low and we tested the recovery of these genes using gradient PCRs (annealing temperatures from 46 to 55°C for mitochondrial and from 52 to 61°C for nuclear), a different number of cycles (25, 35 and 40 cycles) and with and without the Q solution (Qiagen). The optimal conditions were obtained at the same annealing temperatures as those found by Krehenwinkel *et al.* (2018), 46°C for mitochondrial and 55°C for nuclear, but using 40 cycles. Increasing the number of PCR cycles above routine 20-30 cycles is a common practice when working with old-type specimens but can raise the number of polymerase errors. However, a recent publication demonstrated that there is no relationship between the number of PCR cycles (up to 55 cycles were tested) and the number of mutations in the context of high throughput DNA barcoding using Illumina MiSeq sequencing (Vierna *et al.* 2017). Even optimal PCR conditions produced some non-specific amplifications. There were additional amplicons for all the markers except Act5 (see Table S2). These multiple amplifications are related to the design of the primers which are very generalist. However, as we used MiSeq sequencing, these additional amplicons were not considered problematic as we would be able to sort them out of our sequences just by looking at their length + as we are using a 2 x 300 bp chemistry for MiSeq sequencing, longer sequences won't be sequenced.

Finally, all specimens were amplified for the two multiplexes. A selected subset of museum specimens was duplicated during PCR: samples were amplified from different PCR mix, on different days. Controlled were included (PCR mix + water) in each day of amplifications. PCR

products were quantified on an agarose gel relative to a DNA ladder (Promega) and based on band intensity. Based on the relative quantification, we pooled approximately equal amounts of PCR product from the same specimen for the two multiplexes PCR into a single well.

Library preparation, clean-up and sequencing

Samples were transferred to the Human and Environmental Genomic platform of the University of Rennes 1 (Rennes, FRANCE) for library preparation, cleaning and sequencing using MiSeq. PCR products were cleaned of residual primer using 1X AMPure Beads XP (Beckman Coulter). The purified PCR products have been quantified using Quanti-IT Picogreen dsDNA Assay kit (Invitrogen) and qualified using an BioAnalyzer (Agilent). Indexing PCRs of 6-11 cycles were performed using a SmartChip (WaferGen) on pooled amplicons, with indexing primers binding to 5'-tails of the locus-specific PCR primers to introduce dual indexes and Illumina sequencing adapters. For each PCR sample, a unique combination of forward and reverse primers was used so that the sample could later be identified from the sequencing run. The indexed products were cleaned up and quantified by qPCR, then all pooled in equal amounts into a single tube and sequenced on an Illumina MiSeq using V3 (600 cycles) chemistry and 2 x 300 bp reads.

Sequence processing

Sequences were demultiplexed by index barcode combination. We merged paired reads using PEAR (Paired-End reAd mergeR; Zhang *et al.* 2014) with a minimum overlap of 50bp and a minimum quality of Q20. Merged reads were then quality filtered ($\geq 90\%$ of bases $\geq Q30$) and converted into fasta files using the FastX Toolkit (Gordon & Hannon 2010). The resulting fasta files were demultiplexed by primer pair (i.e., target locus), by filtering sequences that start with the forward and end with the reverse primer sequence for each locus. Sequences were clustered into operational taxonomic units (OTUs) using USEARCH (Edgar 2010) at 97% similarity threshold (*cluster_otus*) for COI, Act5, H3, 12S and 16S loci; and treating every truly unique sequence as a separate OTU (*unoise3*), called a zero-radius OTU, for the ribosomal nuclear loci (18S, 28S and ITS2), as they contained heterozygote sequences. A de novo Chimera removal step was included in the clustering. We excluded all OTUs with less than 4-fold coverage. We also excluded all OTUs with less than 10 reads, as 10 reads proved to be sufficient to reliably call consensus sequences from amplicon sequencing data (Henrik Krehenwinkel, comm. pers.). Because of sequencing error, heterozygosity, co-amplification of taxa associated with the targeted spiders, e.g., parasites such as fungi or nematodes, and NUMTs (mitochondrial sequences transposed into the nuclear genome), most of the specimens had more than one OTU for a given marker. The resulting OTU were thus compared against the NCBI nucleotide database using BLASTn (Altschul *et al.* 1990) to filter out non-spider sequences. NUMTs were identified in protein-coding markers (COI, Act5 and H3) by translating the sequences and finding OTU sequences that were interrupted by a stop codon. Some specimens showed spurious amplicons (possibly NUMTs), which were considerably

shorter than the expected length of the sequence. They were also excluded. After these initial filtering steps, it was generally easy to identify the correct OTU as the one with the largest number of reads. After these initial filtering steps, it was easy to identify the correct OTU as the one with the largest number of reads for COI, Act5 and H3. However, for most specimens for the other markers, OTU size was not sufficient to distinguish correct from incorrect OTUs and a neighbor-joining tree was built using all specimens. From these trees, erroneous and heterozygous sequences could be more easily recognized because they fell outside of clades formed by conspecific specimens. Once a single correct sequence had been identified for each marker from each specimen, sequences were aligned in Geneious Prime 2012.2.1 (<https://www.geneious.com>) using the Geneious alignment tool. Alignments were then further checked by hand. Because of incongruencies between mitochondrial genes (although no recombination of the mitochondrial genome of Lycosidae is known), we re-aligned the mitochondrial genes in MEGA7 (Kumar *et al.* 2016) using ClustalW (Thompson *et al.* 1994) with the default values (15 for gap opening and 6.66 for gap extension; 0.5 for transition weight), which were further checked by hand.

Phylogenetic analysis

We analyzed all markers separately to check for incongruencies between loci using Maximum Likelihood (ML) on the CIPRES Science Gateway (<https://www.phylo.org/portal2/home.action>, (Miller *et al.* 2010)). ML phylogenetic reconstructions were first generated using RAxML-HPC v.8 (Stamatakis 2014) but gave low support values (results not shown). We then generated using IQ-Tree 2.1.2 (Nguyen *et al.* 2015) with ultrafast bootstrapping (Minh *et al.* 2013) which allowed us to get slightly more supported nodes of the phylogenetic trees. We used ModelFinder (Kalyaanamoorthy *et al.* 2017) to identify substitution models for each locus (with lowest AICc value, Table 5). Trees were rooted with Hawaiian Lycosidae of another family (supposedly Artoriinae) and the Pisauridae *Bradystichus crispatus*. Trees were edited using TreeGraph 2 (Stöver & Müller 2010).

Results

The wolf spiders collected for this study constitute the most complete collection from the Hawaiian archipelago so far. However, they do not evenly cover the islands of the archipelago nor the elevations. Hence, the phylogenies it depicted are partial views of the actual wolf spider diversity.

Among the 239 Hawaiian wolf spiders that we sequenced, 33 did not work, probably because DNA degradation prevented sequencing, and some contamination. Due to questionable placement, the sequences obtained from a priori Artoriinae, the Museum specimens of *Syroloma* and *Lycosella*, are not included in these preliminary results. However, sequences from fresh non-identified wolf spiders were located out of the tree (and grouped with actual Artoriinae in phylogenetic trees including published sequences, results not shown).

The statistics for each locus are given in Table 5. The different loci were not obtained uniformly for all samples with sequencing success ranging from 21% (Histone 3) to 83% (16S). Considering the very few samples successfully sequenced with Histone 3 and Actin 5, we had to exclude these loci from our analysis. The mitochondrial loci (COI, 12S, and 16S) and the nuclear locus ITS2 present the lowest pairwise identities between sequences (90% to 93%) and will thus probably carry more phylogenetic information than the other loci which are less variable with sequences similar from 96 to 98%.

Table 4: Summary of the characteristics of the nine loci targeted in this study. Sequencing success means the percentage of samples for which sequences we were in good condition enough to be used in the phylogenetic reconstruction compared to the total number of samples for which we got sequences (206). Pairwise identity was calculated by the Geneious software on the alignment of each locus.

	Mitochondrial			ITS2	28S	Nuclear		H3	Act5
	COI	12S	16S			18S_A	18S_B		
Sequencing success (total 206)	76%	73%	83%	68%	63%	71%	79%	21%	28%
Nb of sequences per locus	156	151	172	140	130	146	163	44	57
Pairwise identity of sequences	90.1%	91.4%	93%	92.1%	97.9%	98.1%	98.1%	96%	96.4%
Selected model of substitution (AIC, ModelFinder)	TIM3 + F + I + G4	TIM + F + I + G4	TIM3 + F + G4	TIM2 + F + G4	TN + F + G	TNe + G4	K2P + R2	-	-

Inter- and among islands phylogenetic relationships

When doing the phylogenetic reconstruction for the nuclear loci (ITS2, 28S, 18S_A, and 18S_B), we realized that two different paralogous copies were retained during the OTU selection, for each locus. This was shown by two divergent groups on the trees. Unfortunately, I did not

have time to go back to the OTU selection for these preliminary results. Only a few samples were concerned for the ITS2 and 28S. Thus, I will try to carefully draw up the main patterns given by these phylogenies, considering the two potential copies or excluding the one we consider paralogous. On the opposite, for 18S_A and 18S_B, the samples divide into two copies so we prefer not to interpret their results (but the tree are shown in supplementary material, Figures S2 and S3).

The broad tree topologies obtained by the 7 loci show some incongruities, between mitochondrial and nuclear trees, and in a smaller dimension between mitochondrial trees (see Figures 4 and 5). Consequently, the topology of the COI tree is detailed and the topologies of the trees obtained from the other loci are compared to it as COI is supposed to give the best resolution between closely related species.

Because the surface wolf spiders sequenced were collected from a large range of elevations (see Table 2), three categories of altitudes were arbitrarily defined: low altitude (0-1000m), medium-altitude (1000-2000m), and high altitude (above 2000m), to help the understanding of the phylogenetic patterns.

Mitochondrial loci

COI

The COI tree (Figure 4B), is weakly resolved, which is shown by its short branches. Nonetheless, it shows a hierarchical organization of the spiders from the Hawaiian archipelago. Spiders group according to their habitat (cave vs. surface), island and altitudes with:

- **1.** A group of **cave wolf spiders from the island of Hawaii** (bootstrap: 100) including 3 different cave systems and a surface wolf spider found at low elevation (938 m) in a tropical wet forest of the Mauna Loa volcano (HaML2). This group clusters with the European species *Hogna radiata*.
- And a group of **surface wolf spiders**. This one includes three main groups:
 - **2.** A group of **wolf spiders was found at low altitudes (0-900m)** (bootstrap: 99) **on the islands of Kauai, Oahu, and Molokai**. In this group is found a spider identified as *Hogna crispipes* (OaWa11).
 - **3.** A group of **wolf spiders was found on the island of Maui** (bootstrap: 74).

- A group of **wolf spiders was mainly found on the island of Hawaii** (bootstrap: 85). This group divides into at least 2 sub-groups:
 - One sub-group of spiders coming from the medium to high elevations of the **Mauna Kea and Mauna Loa volcanoes** (bootstrap: 97) splits into two clusters:
 - ❖ 4. One mainly from **high altitudes to summit (2800-4000m) on the Mauna Kea volcano** (bootstrap: 86) which also **includes two spiders from medium altitudes (1220 m)** collected on the Mauna Loa volcano.
 - ❖ 5. One from **medium to high altitudes (1600-3048m) on the Mauna Loa volcano** (bootstrap: 97).
 - One sub-groups of spiders coming from low to high altitudes from the **Mauna Kea, Mauna Loa and Kilauea volcanoes** with low support value (bootstrap: 66) including:
 - ❖ 6. One from **medium to high altitudes (1500-2400m) on the Mauna Kea, Mauna Loa and Kilauea volcanoes** (bootstrap: 95).
 - ❖ 7. One from **low to medium altitudes (900-2400m) of the Kilauea volcano** (bootstrap: 97).
 - ❖ 8. A bush from **medium to high altitude (1524-3000m) of the Mauna Kea and Mauna Loa volcanoes, and from Oahu (OaWa10)**.
 - ❖ 9. A second bush, more basal, **of low to high altitude (950-2400m) from Mauna Loa and Kilauea spiders, including a group (9b) of spiders from low altitude on Kilauea (300m) and medium-altitude on Mauna Loa (1750-2000m)** (bootstrap: 82).

In summary, based on the COI, we distinguish a well-separated lineage of cave spiders and a second lineage of surface spiders. In this surface lineage, we found three groups: one of the spiders from low altitude on the islands of Kauai, Oahu and Molokai; one from the island of Maui; and one of spiders coming mainly from Hawaii.

Comparison of 16S and 12S to the COI tree

The 16S and 12S trees also separate cave from surface wolf spiders (Figure 4, A and C). The placement of the groups and their relationships however are not all the same.

The cave spider group was not well recovered by the tree of the 12S (Figure 4, C), but most of the cave spiders were not successfully sequenced for this locus. 12S does not recover a single cave spiders group but two separate groups, one grouping with the outgroups (HaML1 and HaMK1) (Figure 4C). Interestingly, a surface specimen (HaMK1) from the surface of the Mauna Kea volcano, for which we did not get any sequence with the other mitochondrial loci, groups with a cave spider (HaML1). From the 16S tree, however, we got the same group as with COI, and more resolution was brought by the successful sequencing of a representative of the blind species from the island of Kauai: *Adelocosa anops* (Kauai7).

For surface spiders, 16S does not recover a lineage of mainly Hawaiian spiders as COI and 12S as the Maui group belongs to the same lineage in the 16S tree. Moreover, the two groups that were distinguishable among the Hawaiian surface spiders with COI, one composed of the groups 4 and 5 (high altitude Mauna Kea and Mauna Loa volcanoes) and the other one the groups 6 to 9 (low to high altitude, three volcanoes), differ within the 16S and 12S. With these slowly evolving loci, the two groups are: one composed of group 4, 9 and 5, and the other one of groups 6 to 8. One museum specimen, HaML22 identified as *Hogna oahuensis* (Gertsch determination), was recovered with 12S and 16S and group into group 4. Another museum specimen, Maui 13 identified as *Lycosella* sp., was recovered with 12S and group into the second group of Maui spiders (3b).

Comparison of nuclear 28S and ITS2 to the COI tree

The trees obtained by the nuclear loci 28S and ITS2 are less resolved than the ones obtained by the mitochondrial loci (Figure 5).

The 28S tree (Figure 5A) did not recover all our outgroups with some of the samples which were previously really basal in the mitochondrial trees (e.g., HaMK32) which group within the surface Lycosinae. On the opposite, the cave spiders, be them recovered as a group (bootstrap: 88), is basal to the tree. The surface wolf spider HaML2 which was previously grouping with the cave spiders does not group with them when looking at the 28S tree but is located in between the cave and the surface spiders.

For the ITS2 tree (Figure 5B), some of the outgroups are also located within the surface Lycosinae (e.g., HaMK 32, HaMK33) but the other outgroup specimens are still basal to the tree. The cave spiders are recovered as a separate lineage within the Lycosinae, except for one of the samples (HaML1) which group with the outgroups and with a spider from the surface of the Mauna Kea volcano in particular (HaMK1).

Concerning the surface spiders, most of the groups previously identified with COI, 16S and 12S are not found with the nuclear loci at the exception of the Maui group (bootstrap: 93 for 28S, 70 for ITS2). The group of spiders found at low altitudes on the islands of Kauai, Oahu and Molokai

is not properly recovered as it is split into multiple groups and some of the spiders previously belonging to this group fell into the unresolved bushes of the trees obtained by the nuclear loci. One museum specimen, OaWa7 identified as *Hogna hawaiiensis* (Roth determination), as well as another one identified as *Hogna crispipes* (OaWa2) are recovered into the group of low altitude wolf spiders on the islands of Kauai, Oahu and Molokai with ITS2.

Phylogenetic relationships of the cave wolf spiders

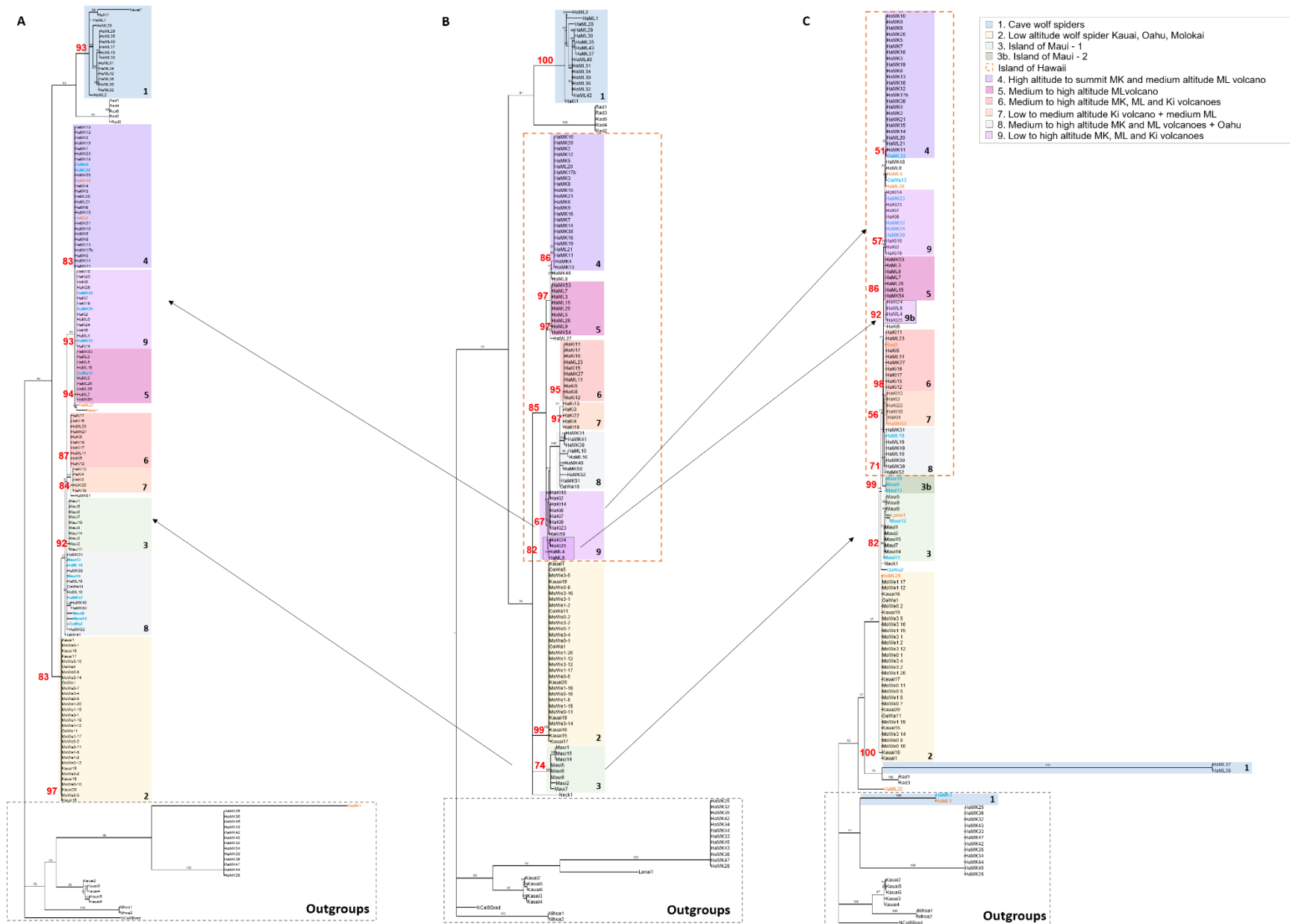
The cave wolf spider group has been recovered with six of the seven loci studied. We here focus on the relationships of the samples using the subtrees obtained from the COI and the 16S loci (Figure 6A and B).

The relationships within the cave lineage follow the cave systems with the spider from the Kaumana cave system (youngest cave studied) being separated from the one from the Keokeo and Kipuka Kanohina Cave systems. The spider from the Keokeo cave system seems to be older than the ones from the Kipuka Kanohina cave system, which is consistent with the age of the caves (see Table 3). We had several samples from the Kipuka Kanohina cave system which, in turn, separate into two groups, with specimens coming from the same cave splitted into these two groups (e.g., HaML34 and HaML35), plus a specimen which is isolated (HaML1).

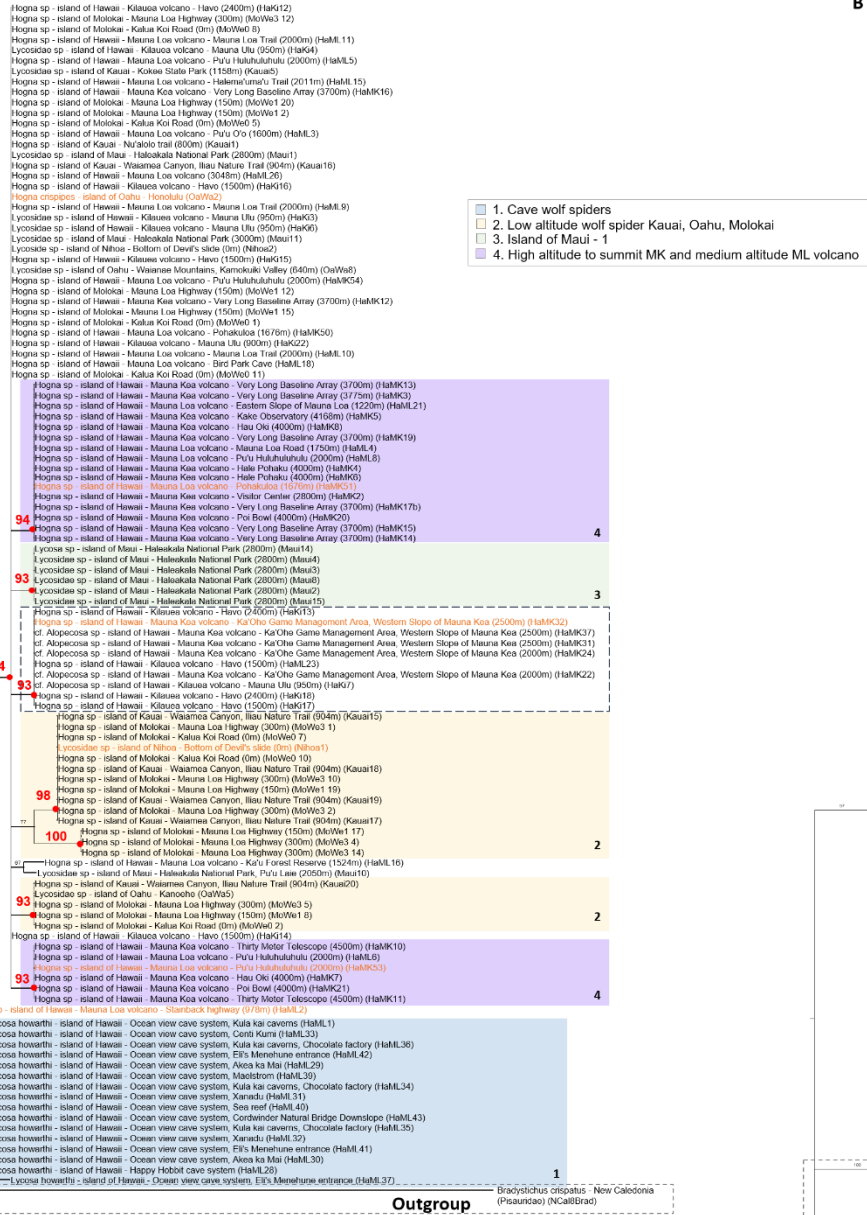
When a sequence of *Adelocosa anops*, the blind cave spider from Kauai, was successfully sequenced (16S, Figure 6B), it fell into the cave group and seems to be related to the spider (HaKi1) from the Kaumana cave (youngest cave studied).

Interestingly, with COI, 16S, and ITS2, the surface spider HaML2, collected on a wet forest at low elevation of Mauna Loa volcano fell into the cave group. With 12S and ITS2, a second surface spider, HaMK1, was collected on the lava flows of the Mauna Kea volcano, group with one spider from the cave system Kipuka Kanohina (HaML1), from the Kula Kai caverns.

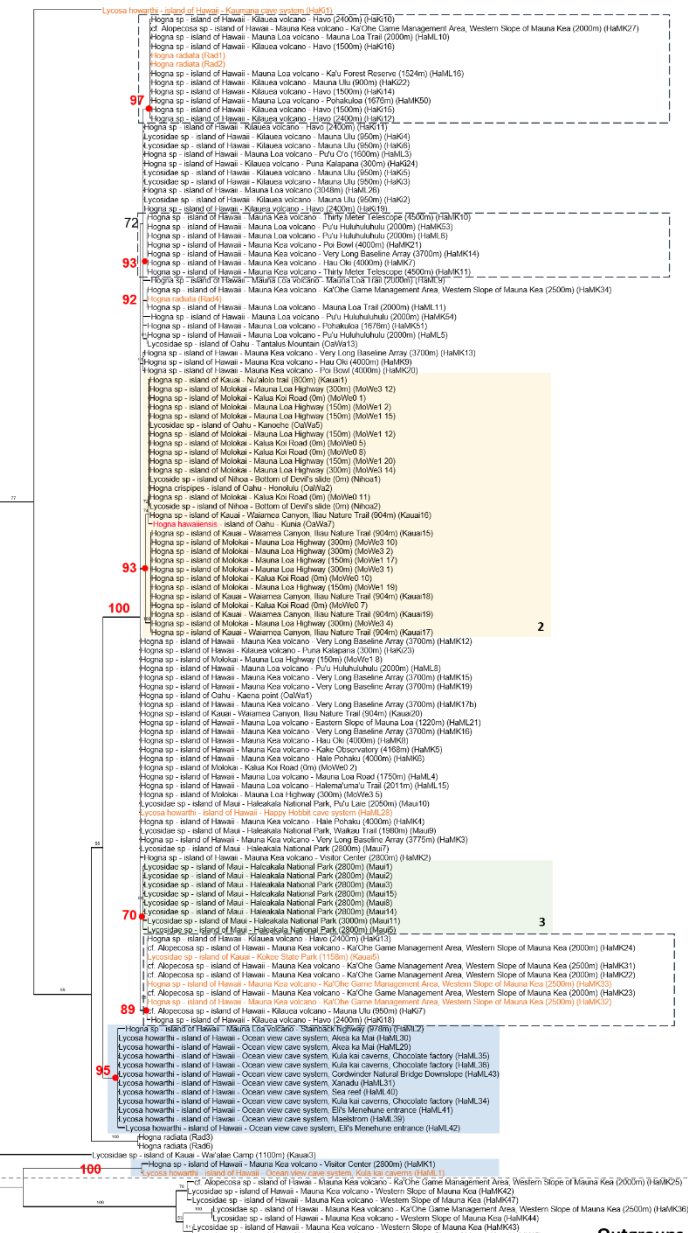
Figure 4: Maximum likelihood phylogeny of Hawaiian wolf spiders from the (A) 16S, (B) COI, and (C) 16 loci. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support value of the groups of interest are highlighted in red. In the 16S and 12S are written in blue the samples which were not successfully sequenced by COI and in orange the samples with different placement. For reasons of space we did not show the information about the samples (identification if ever, location, elevation) but only their code. Their information can be found in Table S1. →



A



B



Outgroup

Outgroups

← **Figure 5:** Maximum likelihood phylogeny of Hawaiian wolf spiders from the A) 28S and, B) ITS2 loci. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support values of the groups of interest are highlighted in red. Are written in orange the samples with different placement compared to COI. The boxes in black dotted lines represent groups that were not recovered by COI nor 16S or 12S.

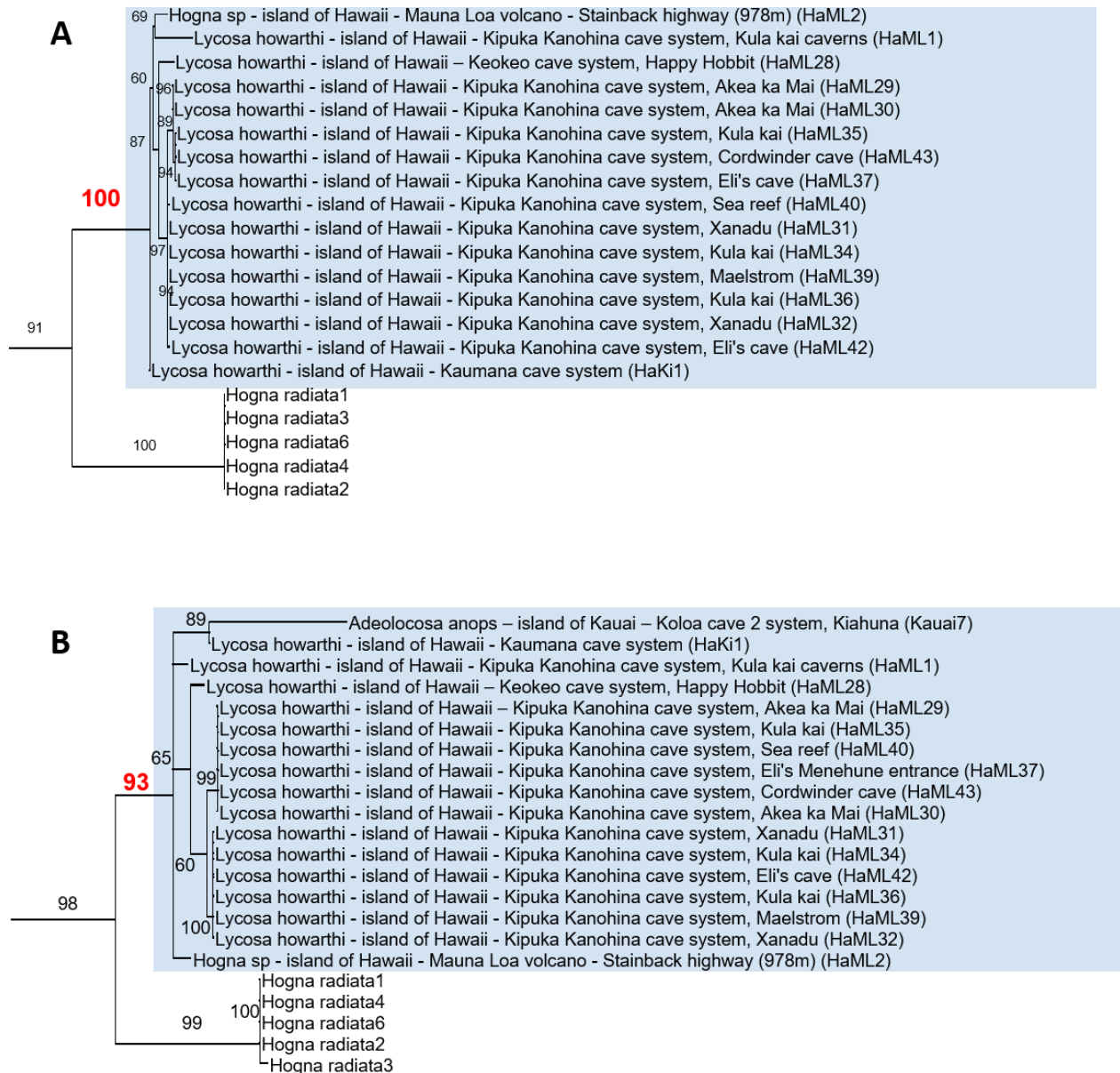


Figure 6: Maximum likelihood phylogeny of the cave wolf spiders from (A) COI and (B) 16S loci. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support values of the group of interest are highlighted in red.

Discussion

Our preliminary phylogenetic analysis of the wolf spiders from the main islands of the Hawaiian archipelago based on COI, 16S, 12S, 28S and ITS2 shows relatively low support and some incongruities between loci (which are discussed in the part Conflicting phylogenies below). Limits between populations and species need to be investigated in the near future (see the perspectives section below).

Phylogenetic relationships

Our phylogenies show relatively low resolution, low support and incongruities between loci. This suggests that (1) the radiation of the Hawaiian wolf spider is recent and the loci we used do not evolve fast enough to carry informative variation and resolve the relationships within this group, and/or (2) there is hybridization between lineages causing gene flow which removes the signal of divergence (Chung & Hey 2017). Because these wolf-spiders are among the first animals to colonize new lava flows (Howarth 1979, Crawford et al. 1995, Edwards & Thornton 2001), we suggest that they may disperse and be able to migrate to new substrates as these become available. Accordingly, the populations found at different elevations along the slope could exchange individuals, arguing in favor of gene flow avoiding divergence. Despite this, the results obtained in this study distinguish some lineages between islands, and between surface and cave spiders.

Overall, the Lycosinae wolf spiders from the Hawaiian Archipelago group all together and are well delimited from the outgroup we used. It splits in two: the surface wolf spiders on one side, the cave wolf spiders on the other. The cave wolf spider lineage has been recovered with six of the seven loci studied. It clusters close to the European species *Hogna radiata*, confirming its belonging to the subfamily Lycosinae (see the perspectives section for further investigation of the taxonomic placement of the Hawaiian wolf spiders). The Hawaiian cave wolf spider *Lycosa howarthi* clusters with the species *Adelocosa anops*, when its sequence was recovered, with little genetic variation, which questions their separation in two different genera.

Between islands

Our phylogenetic analysis recovers lineages with different distributions over the archipelago. One is restricted to the island of Maui. Two species of Lycosinae: *Hogna hawaiiensis* and *Alopecosa oahuensis*, are known from this island. Representatives of these species were included in the phylogenies but did not group within that lineage. We thus hypothesize that the lineage identified restricted to the island of Maui could be a new species, but this needs to be further tested (see the perspectives section). Another lineage recovered by our analysis is spread on the older islands: Kauai, Oahu and Molokai. This lineage presents very few genetic variations even if

it is spread on different islands. Moreover, one of the spiders was identified as *Hogna crispipes*, an introduced species distributed all over the Pacific (although representatives of *H. crispipes* from outside of the Hawaiian archipelago were sequenced but are not recovered within this lineage, results not shown). The specimens sequenced were all from low altitude (but some museum specimens did not have elevation recorded), where there is the most human activity. Consequently, we suggest that this lineage could be recent colonization of the archipelago. A third lineage identified with this phylogenetic analysis is dominated by spiders from the island of Hawaii (which are over-represented in our dataset), but also includes some spiders from Maui and Oahu.

These different aforementioned lineages are from islands of different ages, with the islands of Kauai (5.1 my), Oahu (3.7 my) and Molokai (1.8 my) being older than Maui (1.3 my) and Hawaii (0.5 my). There is however no evidence of progressive colonization of the spiders from the older islands to the youngest islands. Moreover, a lineage contains spiders from old and young islands. Nevertheless, the collection of samples we sequenced, despite containing spiders from almost all the main islands, was not exhaustive (especially because the wolf spiders from the island of Hawaii were over-represented). Nonetheless, in the current state of our understanding, these relationships between the lineages studied here suggest that there might have been several independent colonization of the Hawaiian archipelago by spiders who settled on different islands. The distribution of one lineage between three islands (Kauai, Oahu and Molokai), and the presence of some spiders from Oahu in the lineage identified as mainly from Hawaii highlights a high dispersal capacity. This pattern, if confirmed, will be interesting as different from the progression pattern found for other Hawaiian spider radiations, e.g., *Orsonwelles* (Linyphiidae), *Ariamnes* (Theridiidae), *Mecaphesa* (Thomisidae) and *Tetragnatha* (Tetragnathidae) (Gillespie *et al.* 1997, 2018, Hormiga *et al.* 2003, Garb & Gillespie 2009). A progression rule (or pattern) refers to a phenomenon of phylogeographic concordance with island age, whereby older lineages map to older islands within an archipelago, and younger lineages map to progressively younger islands in that system (Wagner & Funk 1995, Shaw & Gillespie 2016).

Between altitudes

The large sampling of wolf spiders from the island of Hawaii across different volcanoes and a wide range of elevations allowed us to test the hypothesis of differentiation of the Hawaiian wolf spiders according to altitude. The Hawaiian lineage shows a complex phylogenetic pattern with very short branches and variation of groups placement according to the locus studied. Delineation of independent lineages based on the molecular data produced during this study appears difficult. From the mitochondrial loci, we distinguished a group of rather high altitude spiders coming from the volcanoes of Mauna Kea and Mauna Loa and a second from low to high altitudes from the three volcanoes (Mauna Kea, Mauna Loa and Kilauea). Such grouping was not recovered with the nuclear loci, what can be explained by the smaller effective population size of mitochondrial

genes means that makes them coalesce more quickly; and second, by the fact that mitochondrial genes do not recombine. Consequently, there is no clear pattern according to volcano nor altitude, although at least three different bulbs (male genitalia) were observed during previous investigations (Julien Pétilion, comm. pers.). This suggests that the spiders from different elevations and volcanoes might not be fully reproductively isolated from each other and might be still exchanging individuals (and gene flow). Another wolf spider radiation of the genus *Hogna* is known in the Pacific, from the Galapagos archipelago. De Busschere *et al.* (2010, 2012, 2015) found speciation related to habitat specialization (wet habitats vs. upland pampa vs. lowland coastal arid habitats) within islands, repeated on each island of the archipelago, under historic gene flow. This pattern is not found here on the main islands of the Hawaiian archipelago, although they are older (5.1 to 0.6 my) than the Galapagos archipelago (3.2 to 0.7 my), so early colonists of the Hawaiian archipelago could have had more time to diversify. This absence of speciation related to surface habitat specialization on the Hawaiian archipelago could be related to the fact that the surface habitat colonized by wolf spiders are not contrasted enough (high Aeolian vs. neogeoaelian) to cause ecological speciation.

Among the cave spiders

The lineage (mainly composed of *Lycosa howarthi*) shows some genetic variation. The spiders cluster according to their cave system but they also seem to start differentiating within the cave system which was the more covered in our study (Kipuka Kanohina cave system) as some *Lycosa howarthi* collected on the same caves of this system are found to fall into two different groups. A study conducted on Hawaiian cave planthoppers (Wessel *et al.* 2013) showed that these cavernicol exhibit one of the highest speciation rates, suggesting that the conditions down to the Hawaiian caves are conducive to diversification. A study conducted on troglobite spiders of the genus *Dysdera* (Dysderidae) (Arnedo *et al.* 2007) showed that there might be sympatric speciation among troglobitic spiders inhabiting the same caves, potentially through trophic segregation. However, this is unlikely in *L. howarthi* which is known to freely exploit resources in larger cave passages (contrary to other inhabitants of the same caves, see Howarth 1983). On the other hand, cave-adapted species often have reduced dispersal powers (Howarth 1993) and there might also be barriers to subterranean dispersal such as geological structure (Howarth 1983). The Hawaiian caves studied here are part of one of the longest (Kazumura caves) and the third longest (Kipuka Kanohina) cave systems in the world (.). Therefore, we suggest that limited dispersal might be a driver of segregation (not to say speciation, as limits between populations and species have not been tested here).

Our study failed to test the relationship between *Adelocosa anops* and potential surface relatives from the island of Kauai from the few representatives of Kauai we had in our dataset and from the absence of specimens of *Hogna likelikeae*. However, it showed that *Adelocosa anops*

seems to be related to one cave wolf spider from the youngest cave we studied, suggesting colonization of this young cave by a species closer to *Adelocosa anops* than the other *Lycosa howarthi*. Troglobites usually do not disperse on the surface, although such dispersal may occur under species circumstances or as rare chance event (see Howarth 1983 and references therein). It is therefore unlikely that specimens of *Adelocosa anops* colonized this cave.

On this cave lineage are found at least two specimens from the surface of the island of Hawaii. Their presence in this lineage suggests that adaptation to cave environment could be evolutionarily labile for these wolf spiders. It is surprising that on the 133 specimens we gathered from this island, only two seem to be related to the cave lineage. This relationship of surface and cave (*L. howarthi*) wolf spiders from the island of Hawaii, associated with the close relationship of *L. howarthi* with *A. anops* let us suggest that *A. anops* could also be related to surface spiders of its island (Kauai). It is necessary to continue to investigate the relationships between these two troglobitic wolf spiders and their surface relatives with additional sampling from the islands, other than Hawaii. It would also be interesting to including to these investigations specimens of the third known troglobitic wolf spiders, *Nukuhiva adamsoni*, from the Marquesas Islands, to determine how a third event of cave-adapted wolf spiders occurred in the Pacific.

Conflicting phylogenies

The incongruences found on the phylogenies reconstruct from the different loci we targeted illustrated the fact that monophyly depends on the gene region you look at, as impressively shown by the study of 20 genome assemblies in the rapidly radiation *Heliconius* butterflies (Edelman *et al.* 2019).

We observed incongruences among the phylogenies obtained by the different mitochondrial regions we studied. The mitochondrial genomes typically thought not to undergo recombination, so the entire mitogenome should have the same underlying gene tree (Masta 2000, Masta & Boore 2008, Meiklejohn *et al.* 2014). However, it is not rare that mitochondrial regions show incongruencies (Funk & Omland 2003). Part of these incongruities observed between the loci we targeted could be related to the fact that not all the samples were successfully sequenced for all the loci, changing consequently the topologies of the trees obtained from different loci. Another hypothesis explaining the incongruences could be a recombination of the mitochondrial genomes in these spiders. Although mitochondrial recombination may be highest as hybrid zones (Saville *et al.* 1998) and is known from other animals (e.g., birds, Meiklejohn *et al.* 2014), this hypothesis is certainly unlikely.

On the other hand, different genes (or portion of the mitochondrion), may show different speed of evolution (e.g., Mueller 2006). For example, COI is known to evolve faster than 12S and 16S, that could lead of them giving different phylogenetic patterns. Moreover, if the COI loci has been widely used to delimitate species (Hebert *et al.* 2003), it has proven to be problematic in

wolf spiders where it does not recover the species delimited on morphology (Astrin *et al.* 2016, Blagoev *et al.* 2016).

Discordance was also found between the mitochondrial and nuclear loci we targeted. Mitonuclear discordance is common in animals (Toews & Brelsford 2012). Several reasons might explain mitonuclear discordance: the smaller effective population size of mitochondrial genes means that makes them coalesce more quickly; the fact that mitochondrial genes do not recombine, while the nuclear genes do. Additional reasons have been summarized by Ivanov *et al.* (2018) such as horizontal gene transfer (HGT, e.g., Bergthorsson *et al.* 2003, Soucy *et al.* 2015), androgenesis (Hedtke & Hillis 2011), unresolved phylogenetic polytomy (e.g., Caraballo *et al.* 2012), mitochondrial pseudogenes in nuclear DNA (NUMTs) (Leite 2012, Song *et al.* 2014), incomplete lineage sorting (ILS) and introgression (Toews & Brelsford 2012, Mutanen *et al.* 2016), and infection with bacteria like *Wolbachia* (Jiang *et al.* 2018). A recent genomic-scale study focused on mitonuclear discordance in 6 European wolf spider species and showed they were explained by historical or ongoing introgressive hybridization (Ivanov *et al.* 2018), which could also be the case for the Hawaiian wolf spiders.

Perspectives

Analysis done in this study constitute a frame for further studies about phylogenetic relationships among rapidly evolving wolf spider species. These results lead us to propose several avenues for the continuation of this study as well as for future studies.

In the near future, we will be doing additional analysis on these data:

- **Comparing the ML phylogenetic reconstruction with Bayesian reconstructions** (using MrBayes 3.2.7a (Ronquist *et al.* 2012) with 10 million generations) and doing phylogenetic analyses on **concatenated alignments**
- **Reconstructing haplotype network and calculating p-distances** to help to visualize the relationships between individuals, populations, and species intuitively, revealing insights about migration, population structure, and speciation (Garcia *et al.* 2021).
- **Species delimitation using several gene trees** using multispecies coalescent model (MSC) which allows to consider conflicting gene-tree and consequently reliable estimation of the species phylogeny even if the information at every locus is weak (Yang 2015).
- **Dating the speciation**, but it's not always possible to date the splits if there is gene flow.
- Running **Isolation with migration model** to distinguish between population splitting (drift) and gene flow and determine how fast populations diverge (Hey 2010).
- **Including the sequences from the Pacific** (this Ph.D. and Genbank) to test the hypothesis of multiple colonization of the Hawaiian archipelago by wolf spiders as well as the origins of their ancestors.

- **Including the sequences from by Piacentini Ramirez (2019)** who reconstruct the most complete phylogenetic tree of wolf spiders so far, including representatives of each subfamily. This will allow to determine the taxonomic placement of our wolf spiders.

We suggest the coming studies focusing on Hawaiian wolf spiders, or other potentially recent radiation of a young lineage to use genome-wide Next-Generation-Sequencing (NGS) to get a better resolution of the phylogenetic relationships. Among the myriad of NGS available, we consider that:

- (1) genome sequencing seems hardly reachable because of the cost and the difficulty to sequence so many samples, which will be necessary in similar cases where morphological conservatism does not allow previous taxonomic knowledge about the studied group.
- (2) enrichment, e.g., using Ultra conserved Elements (UCE), which has greatly helped the resolution of the spider tree of life recently (e.g., Kulkarni *et al.* 2020).
- (3) transcriptomes sequencing (Garrison *et al.* 2016, Fernández *et al.* 2018, Kallal *et al.* 2021) to resolve deep phylogenomic relationships between the Pacific wolf spiders.
- (4) RAD tags: which is a popular method for population genetic and phylogeographic studies and is preferred over microsatellites approaches because of the limitations of their development due to the difficulty to find reliable loci (Brewer *et al.* 2014). Additionally, this method has recently proven to be relevant to delimit species and populations of closely related wolf spiders (De Corte 2016, Ivanov *et al.* 2021).
- (5) Genome skimming: which allows the assembly of plastid or mitochondrial genomes which is cheaper than any of the approaches mentioned before and would allow to sequence degraded DNA, such as from museum specimens (Coissac, Hollingsworth, Lavergne, & Taberlet 2016, Dodsworth 2015).

Conclusion

Finally, this study was the first to investigate the relationships among the Hawaiian surface and caves wolf spiders coming from different islands. The preliminary results presented here showed recent radiation driven by dispersal and habitat speciation likely mixed by gene flow. We found an independent lineage of cave spiders including some surface spiders suggesting that adaptation to cave is quite evolutionarily labile for these spiders. No clear pattern of elevational speciation was found but further analyzes are needed to better understand the situation.

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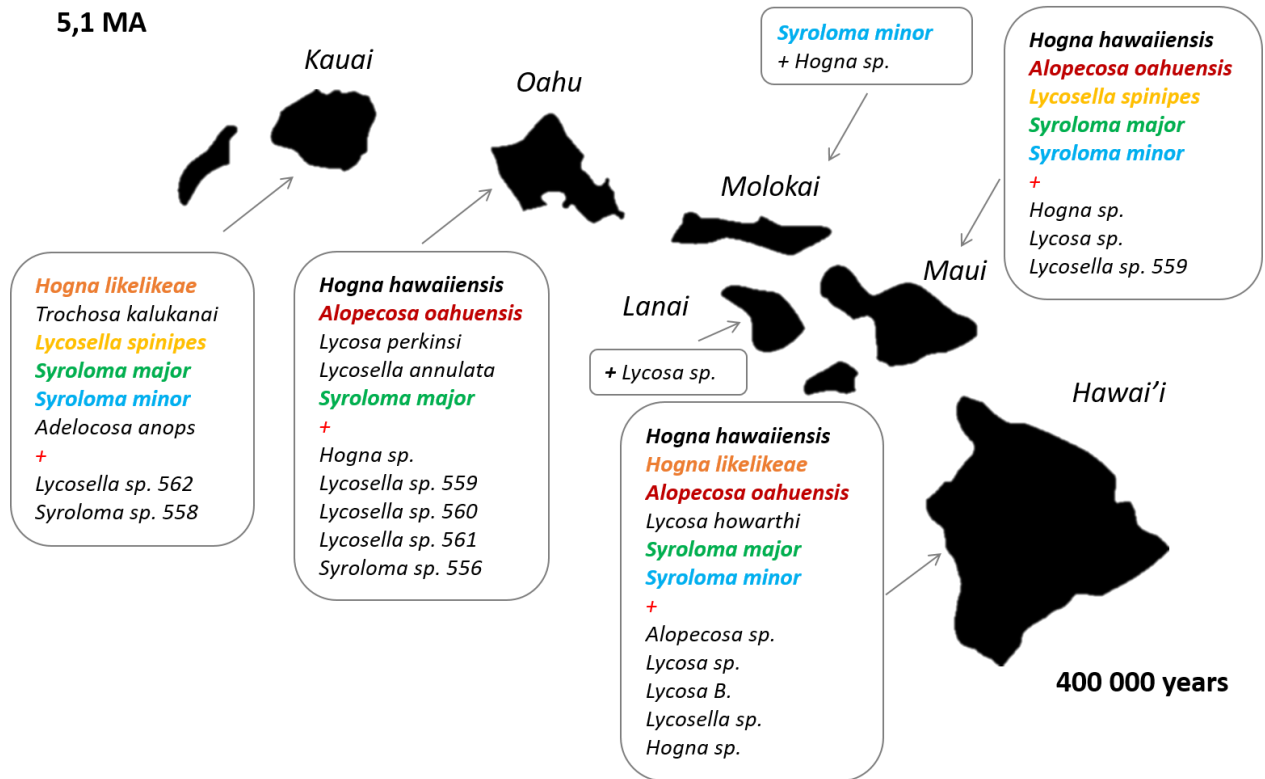
Supplementary materials

Figure S1: Map of the islands of Hawaii showing the known repartition of the species described to date

Table S1: Details about the specimens sequenced in this study.. *: samples duplicated during PCR, Det.: determination, Elev.: elevation.

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
B76-1 *	-	-	female	Hawaii	Gardner Pinnacles	-	-	-	-	-	1971	Ken Norris	Bishop Museum
Hahua1	-	-	juv	Hawaii	Hawaii	Hualalai	Kealakekua Ranch cave	Cave	-	1310	1972	J. Jacobi, F.G. Howarth	Bishop Museum
HaKi1	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Kilauea	Kaumana Cave	Cave	N19.487° W155.049°	400	2016	Jesse Eiben - Kyle Davis	Bishop Museum
HaKi2	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi3	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi4	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi5	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi6	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi7	Alopecosa ?	sp1	juv	Hawaii	Hawaii	Kilauea	Volcanoes Park (Napau Crater Trail)	Forest	N19.370064° W155.213422°	980	2015	Andy Rominger	Field collection
HaKi8	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi9	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi10	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi11	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi12	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi13	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi14	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
HaKi15	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi16	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi17	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi18	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi19	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi20 *	-	-	female	Hawaii	Hawaii	Kilauea	Ainahou	-	-	975	1974	W.P. Mull	Bishop Museum
HaKi21 *	-	-	juv	Hawaii	Hawaii	Kilauea	Kilauea Iki Center	Under rock	-	1097	1977	W.P. Mull	Bishop Museum
HaKi22 *	-	-	male	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu flow	-	-	900	1980	-	Bishop Museum
HaKi23	-	-	female	Hawaii	Hawaii	Kilauea	Puna Kalapana	-	-	304	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi24	-	-	female	Hawaii	Hawaii	Kilauea	Puna Kalapana	-	-	304	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi25	-	-	juv	Hawaii	Hawaii	Kilauea	Puna Kalapana	-	-	304	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi26 *	-	-	juv	Hawaii	Hawaii	Kilauea	Kazumura cave	Cave	-	-	1971	F.G. Howarth	Bishop Museum
HaKi27 *	-	-	juv	Hawaii	Hawaii	Kilauea	Kazumura cave	Cave	-	-	1971	F.G. Howarth	Bishop Museum
HaMK1	-	-	juv	Hawaii	Hawaii	Mauna Kea	Visitor Center	-	N19.75616583° W155.4589439°	2800	2016	Julien Pétilion	Field collection
HaMK2	-	-	female	Hawaii	Hawaii	Mauna Kea	Trail from the Mauna kea Visitor Center	Alpine Stone Desert	N19.75616583° W155.4589439°	2800	2016	Julien Pétilion	Field collection
HaMK3	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Kea	Mauna Kea	Alpine Stone Desert	N19.79972° W155.45651°	3775	2014	Jesse Eiben	Paul Blanko
HaMK4	-	-	female	Hawaii	Hawaii	Mauna Kea	Hale Pohaku	-	N19.82189° W155.46895°	4000	2015	Jesse Eiben	Field collection
HaMK5	cf. Alopecosa	sp1	male	Hawaii	Hawaii	Mauna Kea	Mauna Kea	Alpine Stone Desert	N19.82550° W155.47514°	4168	2014	Jesse Eiben	Field collection

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
HaMK6	-	-	juv	Hawaii	Hawaii	Mauna Kea	Hale Pohaku	-	N19.81945° W155.46454°	4000	2015	Jesse Eiben	Field collection
HaMK7	Lycosa	sp 1	male	Hawaii	Hawaii	Mauna Kea	Hau Oki	Alpine Stone Desert	-	-	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK8	Lycosa	sp 1'	male	Hawaii	Hawaii	Mauna Kea	Hau Oki	Alpine Stone Desert	N19.82190° W155.46875°	-	2015	Jesse Eiben	Field collection
HaMK9	Lycosa	sp B	female	Hawaii	Hawaii	Mauna Kea	Hau Oki	Alpine Stone Desert	-	-	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK10	Lycosa	sp	male	Hawaii	Hawaii	Mauna Kea	TMT	Alpine Stone Desert	-	-	2018	Jesse Eiben	Field collection
HaMK11	Lycosa	sp 1'	male	Hawaii	Hawaii	Mauna Kea	TMT	Alpine Stone Desert	-	-	2018	Jesse Eiben	Field collection
HaMK12	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	North VLBA	Alpine Stone Desert	-	-	2016	Jesse Eiben - Julien Pétillon	Field collection
HaMK13	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	-	3700	2018	Jesse Eiben	Field collection
HaMK14	Lycosa	Lycosa sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2016	Jesse Eiben - H. Stever	Field collection
HaMK15	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2018	Jesse Eiben	Field collection
HaMK16	Lycosa	sp B	female	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK17b	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2018	Jesse Eiben	Field collection
HaMK18	Lycosa	sp A	female	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2016	Jesse Eiben	Field collection
HaMK19	Lycosa	sp A	female	Hawaii	Hawaii	Mauna Kea	VLBA	Alpine Stone Desert	-	-	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK20	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	Poi Bowl	Alpine Stone Desert	N19.82354° W155.47536°	4000	2016	Jesse Eiben - Julien Pétillon - H. Stever	Field collection
HaMK21	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	Poi Bowl	Alpine Stone Desert	N19.82354° W155.47536°	4000	2016	Jessen Eiben	Field collection

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
HaMK22	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1994	Paul Blanko	Paul Blanko
HaMK23	cf. Alopecosa	sp1	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1994	Paul Blanko	Paul Blanko
HaMK24 *	cf. Alopecosa	sp3	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1992	Paul Blanko	Paul Blanko
HaMK25	cf. Alopecosa	sp3	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1995	Paul Blanko	Paul Blanko
HaMK26	cf. Alopecosa	sp3	-	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1995	Paul Blanko	Paul Blanko
HaMK27 *	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	6/14/1905	Paul Blanko	Paul Blanko
HaMK28	cf. Alopecosa	sp3?	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1993	Paul Blanko	Paul Blanko
HaMK29	-	-	-	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1993	Paul Blanko	Paul Blanko
HaMK30	-	-	-	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1993	Paul Blanko	Paul Blanko
HaMK31	cf. Alopecosa	sp3?	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK32	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK33	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK34	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK35	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK36	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
HaMK37	cf. Alopecosa	sp3	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8285373612424 68° W155.571056349430 36°	2500	1993	Paul Blanko	Paul Blanko
HaMK38 *	cf. Alopecosa	sp1?	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1992	Paul Blanko	Paul Blanko
HaMK39	cf. Alopecosa	sp3	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1995	Paul Blanko	Paul Blanko
HaMK40	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1995	Paul Blanko	Paul Blanko
HaMK41	-	-	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1995	Paul Blanko	Paul Blanko
HaMK42 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK43 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK44 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK45 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK46	-	-	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK47 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK48	Lycosa	Lycosa B	male	Hawaii	Hawaii	Mauna Kea	Pu'u Huluhulu	-	-	-	1995	-	Bishop Museum
HaMK49	-	-	female	Hawaii	Hawaii	Mauna Kea	Pohakuloa	-	-	-	1992	Gordon	Bishop Museum
HaMK50	-	-	female	Hawaii	Hawaii	Mauna Kea	Bobcat trail, Pohakuloa training area	-	-	1676	1995	Howarth	Bishop Museum
HaMK51	-	-	female	Hawaii	Hawaii	Mauna Kea	Bobcat trail, Pohakuloa training area	-	-	1676	1995	Howarth	Bishop Museum
HaMK52	Lycosa	Lycosa sp a	juv	Hawaii	Hawaii	Mauna Kea	Mauna Kea Forest Reserve	-	19°47'N, 155°36'W	1880	2002	P. Krushelnyc ky coll.	Bishop Museum

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HaMK53	-	-	female	Hawaii	Hawaii	Mauna Kea	Pu'u Huluhulu	-	-	2040	2003	-	Bishop Museum
HaMK54	-	-	juv	Hawaii	Hawaii	Mauna Kea	Pu'u Huluhulu	-	-	2040	2003	-	Bishop Museum
HaML1*	Lycosa	cf Lycosa howarthi (no eye)	female	Hawaii	Hawaii	Mauna Loa	Kula Kai Caverns	Cave	N19.11917° W155.77645°	900	-	Asa Aue, F. Stone	Essig Museum
HaML2	cf. Alopecosa	sp2	female	Hawaii	Hawaii	Mauna Loa	Stainback highway	Forest	N19.57418° W155.21587°	978	2015	Andy Rominger	Field collection
HaML3	-	-	male	Hawaii	Hawaii	Mauna Loa	Pu'u O'o	Lava flow	N19.67174° W155.34570	1600	2016	Julien Pétillon - Jesse Eiben	Field collection
HaML4	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.47585° W155.36391°	1750	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML5	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.686392° W155.465047°	2000	2012	Jesse Eiben	Field collection
HaML6	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.686392° W155.465047°	2000	2012	Jesse Eiben	Field collection
HaML7	-	-	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.68696° W155.46407°	2000	2016	Jesse Eiben - Julien Pétillon - Heather Stever	Field collection
HaML8	-	-	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.68696° W155.46407°	2000	2016	Jesse Eiben - Jorden Zarders	Field collection
HaML9	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.49270° W155.38550°	2000	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML10	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.49270° W155.38550°	2000	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML11	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.49270° W155.38550°	2000	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML15	-	-	-	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu saddle road	-	N19.411324° W155.275054°	2011	2016	Jesse Eiben	Field collection
HaML16	-	-	juv	Hawaii	Hawaii	Mauna Loa	Kau Forest Reserve	-	-	1524	2004	S. Benjamin	Essig Museum
HaML17 *	-	-	male	Hawaii	Hawaii	Mauna Loa	Volcano Hongo Store Cave	-	-	-	1971	F.G. Howarth, J. Jacobi	Bishop Museum
HaML18 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Bird Park Cave, kipuka Puauulu, Mauna Loa	-	-	1140	1971	F.G. Howarth	Bishop Museum

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HaML19 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Bird Park Cave, kipuka Puauulu, Mauna Loa	-	-	1140	1971	F.G. Howarth	Bishop Museum
HaML20 *	-	-	female	Hawaii	Hawaii	Mauna Loa	E slope of Mauna Loa	-	-	1220	1971	-	Bishop Museum
HaML21 *	-	-	male	Hawaii	Hawaii	Mauna Loa	Mauna Loa, east slope, treemold area	-	-	1220	1971	J. Jacobi	Bishop Museum
HaML22 *	Lycosa	Lycosa oahuensis (Gertsch det.)	female	Hawaii	Hawaii	Mauna Loa	Havo, Strip Road	-	-	1463	1974	W.P. Mull	Bishop Museum
HaML23	-	-	male	Hawaii	Hawaii	Mauna Loa	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaML24	-	-	female	Hawaii	Hawaii	Mauna Loa	Havo, Mauna Loa strip road	-	-	1584	-	W. Gagné, F. Howarth	Bishop Museum
HaML25 *	-	-	female	Hawaii	Hawaii	Mauna Loa	Power Line Road	-	-	1706	1978	W.P. Mull	Bishop Museum
HaML26 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa	-	-	3048	1980	D. Boyton	Bishop Museum
HaML27 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Summit, near 1949 cone (1/4 mile)	Lava flow	-	4053	1980	Richard P.	Bishop Museum
HaML28	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina, Happy Hobbit	Cave	-	-	2015	ME Slay, C Slay, ML Porter	Field collection
HaML29	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Akea Ka Mai	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML30	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Akea Ka Mai	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML31	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Xanadu	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML32	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Xanadu	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML34	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Kula Kai; Chocolate factory	Cave	-	-	2017	ML Porter, SA Engel, AS Engel, P Bosted	Field collection
HaML35	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Kula Kai; Chocolate factory	Cave	-	-	2017	ML Porter, SA Engel, AS Engel, P Bosted	Field collection

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HaML36	Lycosa	Lycosa howarthi	male	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Kula Kai; Chocolate factory	Cave	-	-	2017	ML Porter, SA Engel, AS Engel, P Bosted	Field collection
HaML37	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	ML Porter, AG Hudson, V Hackell, T Gracinin, S Engel	Field collection
HaML39	Lycosa	Lycosa howarthi	-	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Maelstrom	Cave	-	-	2017	CAM Slay, AS Engel, V Hackell, ML Porter, ME Slay, SA Engel	Field collection
HaML40	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Sea reef	Cave	-	-	2018	B Chong, A Hudson, ML Porter, R Thomson	Field collection
HaML41	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	B Chong, A Hudson, ML Porter, R Thomson	Field collection
HaML42	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	M Slay, Scott Engel, A Katz, S Taylor	Field collection
HaML43	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Cordwinder Natural Bridge Downslope (station 41-43)	Cave	-	-	2018	A Engel, S Engel, J Jacoby, S Taylor	Field collection
HaML44	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	S Engel, J Jacoby, S Taylor	Field collection
Kauai1	-	-	male	Hawaii	Kauai	-	Nu'alolo trail - Na Pali Kona	Under dirt clump of side of trail	N22.08716° W159.41440°	800	2016	-	Field collection
Kauai2	-	-	juv	Hawaii	Kauai	Kokee State Park	Nualolo trail	-	-	1000	2000	Arnedo, Hormiga & Agnarsson	Essig Museum
Kauai3	-	-	juv	Hawaii	Kauai	Wai'alaie Camp	Camp	-	-	1100	2000	Arnedo, Hormiga & Agnarsson	Essig Museum

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Kauai4	-	-	juv	Hawaii	Kauai	Wai'alaie Camp	Wai'alaie Camp	-	-	1100	2000	Arnedo, Hormiga & Agnarsson	Essig Museum
Kauai5	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee	-	-	1158	2004	S.L. Montgomery	Essig Museum
Kauai6	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee	-	-	1158	2004	S.L. Montgomery	Essig Museum
Kauai7 *	-	-	femal e	Hawaii	Kauai	Kiahuna	Kiahuna	-	-	-	1979	-	Bishop Museum
Kauai8 *	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee	Woodlan d	-	-	1963	-	Bishop Museum
Kauai9 *	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee Park	Woodlan d	-	-	1964	T. Suman	Bishop Museum
Kauai10 *	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee State Park	-	-	1140	1973	F.G. Howarth	Bishop Museum
Kauai11 *	Adelocosa	Adelocosa anops	femal e	Hawaii	Kauai	Koloa, Koloa Cave#2	Koloa, Koloa Cave#2	Cave	-	-	1971	F.G. Howarth	Bishop Museum
Kauai12 *	-	-	juv	Hawaii	Kauai	Koloa, Koloa Cave#2	Koloa, Koloa Cave#2	Cave	-	-	1971	F.G. Howarth	Bishop Museum
Kauai13 *	-	-	femal e	Hawaii	Kauai	Koloa, Koloa Cave#2	Koloa, Koloa Cave#2	Cave	-	-	1971	F.G. Howarth	Bishop Museum
Kauai14	Hogna	Hogna sp.	male	Hawaii	Kauai	Lihue airport	Lihue airport	-	-	-	1993	Mike Linnell + Dean Jamieson	Bishop Museum
Kauai15	Hogna	-	juv	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai16	Hogna	-	juv	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai17	Hogna	-	male	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai18	Hogna	-	femal e	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai19	Hogna	-	juv	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Kauai20	Hogna	-	female	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Lanai1 *	Lycosa	Lycosa 1	male	Hawaii	Lanai	Pamoi	Pamoi	On loess	-	457	1973	S.L. Montgomery	Bishop Museum
Lays2 *	Alopecosa	Lycosa oahuensis (Gertsch det.)	juv	Hawaii	Laysan	-	-	Dead albatros	-	-	1959	-	Bishop Museum
Lays3 *	-	-	juv	Hawaii	Laysan	At campsit e	At campsite	-	-	-	1987	Marie Maie (?)	Bishop Museum
Lycoannu1 *	Lycosella	Lycosella annulata	juv	Hawaii	Oahu	-	Honolulu	-	-	-	-	Perkins	MNHN
Lycosp1 *	Lycosella	Lycosella sp	juv	Hawaii	-	-	-	-	-	-	-	Perkins	MNHN
Lycospini1 *	Lycosella	Lycosella spinipes	juv	Hawaii	Maui	-	Haleakala	-	-	-	-	Perkins	MNHN
Maui1	-	-	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui2	-	-	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui3	-	-	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui4	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui5	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui6	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui7	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui8	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui9	-	-	female	Hawaii	Maui	Haleakala	East Maui, Waikau trail, Haleakala Nat. Park	-	-	1980	1996	Howarth	Bishop Museum
Maui10 *	-	-	juv	Hawaii	Maui	Haleakala	East Maui, Haleakala Nat. Park, Puu Laie	Bush	-	2050	1976	F.G. Howarth	Bishop Museum

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Maui11 *	-	-	male	Hawaii	Maui	Haleakal a	East Maui, Haleakala Nat. Park	-	-	3000	1980	W.C. Gagné	Bishop Museum
Maui12 *	-	-	femal e	Hawaii	Maui	Haleakal a	Rainforest	-	-	-	1980	R. Warshauer	Bishop Museum
Maui13 *	Lycosella	Lycosella imm.	juv	Hawaii	Maui	Haleakal a	Haleakala Nat. Park	Forest	20°44'N, 156°14'W	1859	1981	W.C. Gagné	Bishop Museum
Maui14	Lycosa	Lycosa sp	male	Hawaii	Maui	Haleakal a	Haleakala Nat. Park	-	20°44'N, 156°14'W	2800	2003	P. Krushelnyc ky coll.	Bishop Museum
Maui15	-	-	male	Hawaii	Maui	Haleakal a	Haleakala Nat. Park	-	20°44'N, 156°14'W	2800	2003	P. Krushelnyc ky coll.	Bishop Museum
Maui16 *	-	-	male	Hawaii	Maui	Haleakal a	East Maui, Waikau trail, Haleakala Nat. Park	-	-	2000	1976	F.G. Howarth, R.C.A. Rice	Bishop Museum
Maui17 *	-	-	male	Hawaii	Maui	Haleakal a	East Maui, Haleakala Nat., Silverwood	-	-	-	1975	F.G. Howarth	Bishop Museum
Maui18 *	-	-	male	Hawaii	Maui	Haleakal a	East Maui, Haleakala Nat. Park	-	-	3000	1975	W.C. Gagné	Bishop Museum
MoWe0-1	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-10	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-11	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-2	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-5	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-7	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-8	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe1-12	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
MoWe1-15	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-17	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-19	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-2	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-20	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-8	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe3-1	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-10	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-12	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-14	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-2	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-4	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-5	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
NCal8Brad*	Bradystichus	Bradystichus crispatus	female	New Caledonia	New Caledonia	-	29 a Mt. Mé Ori, pente SE	Forest	165°40'22"E 21°32'18"S	530	1987	A & S Tillier	MNHN
Neck1*	-	-	juv	Hawaii	Necker	Hawaii Isl. (?)	Hawaii Isl. (?)	-	-	-	1982	P. Conant	Bishop Museum
Neck2*	-	-	female	Hawaii	Necker	Hawaii Isl. (?)	Hawaii Isl. (?)	-	-	-	1982	P. Conant	Bishop Museum
Neck3*	-	-	male	Hawaii	Necker	Hawaii Isl. (?)	Hawaii Isl. (?)	-	-	-	1982	P. Conant	Bishop Museum
Nihoa1*	?	-	juv	Hawaii	Nihoa	-	Bottom of Devil's Slide	-	N23.0633° W161.9262°	0	2016	Sheldon Plentovich	Field collection

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Nihoa2	?	-	juv	Hawaii	Nihoa	-	Bottom of Devil's Slide	-	N23.0633° W161.9262°	0	2015	Sheldon Plentovich	Field collection
OaWa1*	-	-	female	Hawaii	Oahu	Waiana'e	Kaena Point	-	-	-	2015	P. Kruselnycky	Bishop Museum
OaWa2*	-	-	female	Hawaii	Oahu	Honolulu	Honolulu, Kalihi, Bishop Museum grounds	Lawn	-	-	1983	F.G. Howarth, W.G. Gagné	Bishop Museum
OaWa3*	Hogna	Hogna crispipes	female	Hawaii	Oahu	Honolulu	Honolulu	-	-	-	1965	A. Miyaharo	Bishop Museum
OaWa4	Hogna	Hogna crispipes	male	Hawaii	Oahu	Kahuluu	Kahuluu	-	-	-	1993	-	Bishop Museum
OaWa5	Hogna	Hogna crispipes	female	Hawaii	Oahu	Kanoeh'e, near Vall. of temples	Kanoeh'e, near Vall. of temples	Outside house	-	-	1993	-	Bishop Museum
OaWa6*	-	-	male	Hawaii	Oahu	Ko'olau	Koolau Mts, Poamoho trail	-	-	700	1977	F.G. Howarth	Bishop Museum
OaWa7*	Hogna	Lycosa hawaiiensis (Roth det.)	female	Hawaii	Oahu	Kunia, Village Park	Kunia, Village Park	-	-	-	1988	F.G. Howarth	Bishop Museum
OaWa8*	-	-	juv	Hawaii	Oahu	Waiana'e	Waiana'e Mts, Kamokuiki Valley	-	-	640	1933	E.H. Bryan Jr	Bishop Museum
OaWa9*	Lycosella	Lycosella sp	juv	Hawaii	Oahu	Waiana'e	Waiana'e Mts, Palikea trail	-	-	650	1980	W.C. Gagné	Bishop Museum
OaWa10*	-	-	juv	Hawaii	Oahu	Waiana'e	Waiana'e Kai Valley	Woodland	-	650	1974	F.G. Howarth, W.G. Gagné	Bishop Museum
OaWa11*	Hogna	Hogna crispipes	male	Hawaii	Oahu	Waipahu	Waipahu	-	-	-	-	Anita Manning	Bishop Museum
OaWa12*	-	-	male	Hawaii	Oahu	Ko'olau	Koolau Mts, Poamoho trail	Under leaves	-	summit	1980	J. Obata	Bishop Museum
OaWa13*	Lycosella	Lycosella sp. (Roth det.)	juv	Hawaii	Oahu	Ko'olau	Tantalus Mt., Ko'olau	Litter in stream bed	-	-	1964	-	Bishop Museum
Rad1	Hogna	Hogna radiata	male	Europe	Europe	-	Dunes Erdeven (56)	Dune	-	-	2004	Cyril Courtial	Gretia
Rad2	Hogna	Hogna radiata	female	Europe	Europe	-	Dunes Erdeven (56)	Dune	-	-	2004	Cyril Courtial	Gretia
Rad3	Hogna	Hogna radiata	female	Europe	Europe	-	Dunes Hoedic (56)	Dune	-	-	2011	Mathieu Lagarde	Gretia
Rad4	Hogna	Hogna radiata	female	Europe	Europe	-	Dunes Guérande (44)	Dune	-	-	2012	Cyril Courtial	Gretia

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Rad6	Hogna	Hogna radiata	male	Europe	Europe	-	Koh Kastell, Belle ile (56)	Lawn	-	-	2000	-	Gretia
Syromin1*	Syroloma	Syroloma minor	male	Hawaii	-	-	-	-	-	-	-	Perkins	MNHN
Syromin2*	Syroloma	Syroloma minor	juv	Hawaii	-	-	-	-	-	-	-	Perkins	MNHN

Table S2: Sizes of the additional amplicons obtained during PCR amplifications and observed on agarose gel

Region	ID	Length (bp)	Size of the multiple amplicons	Average amplicon length
Mitochondrial	COI	365	1000 bp	318
			400 bp	
	CytB	401	450 bp	-
	12S	424	1300 bp	400
			1000 bp	
			900 bp	
			800 bp	
	16S	371	1000 bp	315
400 bp				
Nuclear	18S_A	421	1000 bp	371
			500 bp	
	18S_B	351	900 bp	272
			400 bp	
	28S	363	950 bp	314
			450 bp	
	ITS2	436	1000bp	435
			600 bp	
			500 bp	
	H3	374	650 bp	328
450 bp				
Act5	270	450 bp	226	

18S_A

When doing the phylogenetic reconstruction for the 18S_A (Figure S2), I realized that there were probably two different paralog copies that were selected during the OTU selection. This was shown by two really divergent groups on the tree: one containing 42 samples and the other one 97 samples (apart from the outgroups that contains 7 samples). As previously mentioned, we did not have time to go back to the OTU selection for these preliminary results but we couldn't exclude that much sequences from our analysis. Thus, we will here try here to carefully draw up the main patterns given by this phylogeny, considering the two potential copies (referred as upper and lower copy, from their position in the phylogenetic tree).

Overall, the main difference of the phylogeny given by 18S_A compared to the one given by the other loci is its really low resolution with almost all the samples sequenced included in the same bush (in either of the two potential paralogous copies of the gene).

In the group formed by the **upper copy** are found the **cave wolf spiders** and **epigean wolf spiders**. Among the 14 specimens for which we get 18S_A sequences, seven group together in a separated group (blue, bootstrap: 92), and the seven others (names written in red, from Kaumana cave system HaKi1, and from Kipuka Kanohina cave system: HaML1, HaML28, HaML42, HaML32, HaML29, HaML39, HaML37) are in a bush with all the epigean spiders, from the European *Hogna radiata* to wolf spiders found on the islands of Maui, Kauai, Oahu, Nihoa, Hawaii, from low to high elevations (0-4168m).

In the group formed by the **lower copy** are only found epigean wolf spiders from the Hawaiian archipelago. They are separate in three groups including:

- a bush of mainly **low elevations wolf spiders (0-900m) from the islands of Kauai, Oahu and Molokai** and two high elevation spiders from the island of Maui.
- A group of low to medium elevation wolf spiders (300-2500m) from Kilauea and Mauna Kea volcanoes (bootstrap: 99).
- A group of medium to high elevations wolf spiders (1158-4000m) from the Mauna Kea volcano on the island of Hawaii and the island of Kauai (bootstrap: 92).

18S_B

When doing the phylogenetic reconstruction for the 18S_B (Figure S3), I realized that there were as well probably two different paralog copies that were selected during the OTU selection. This was shown by two divergent groups on the tree: one containing 31 samples and the other one 131 samples. As previously mentioned, we did not have time to go back to the OTU selection for this preliminary results but we couldn't exclude that much sequences from our analysis. Thus we will here try here to carefully draw up the main patterns given by this phylogeny, considering the two potential copies (referred as upper and lower copy, from their position in the phylogenetic tree).

In the group formed by the upper copy are found wolf spiders from the European species *Hogna crispipes* as well as from all the Hawaiian Islands and all the elevations, including two cave wolf spiders (one from Kaumana cave system (HaKi1), one from Kipuka Kanohina cave system (HaML1)). Part of our outgroup wolf spiders (supposedly Artoriinae) group outside of this upper copy.

In the group formed by the lower copy are found two main groups (bootstrap: 97):

- One of epigeal wolf spiders in which we distinguish two sub-groups:
 - A bush of wolf spiders from the islands of Oahu and Hawaii (low to medium elevations: 900-2500m)
 - A group of low elevation (0-904m) wolf spiders from Kauai, Oahu, Nihoa and Molokai (bootstrap: 94).
- One of cave wolf spiders from the island of Hawaii, cave system "Kipuka Kanohina" (bootstrap: 99).



Figure S3: Maximum likelihood phylogeny of Hawaiian wolf spiders from the 18S_B locus. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support value of the groups of interest are highlighted in red.

GENERAL DISCUSSION AND PERSPECTIVES

General discussion: habitat plays a role in tropical spider diversity

Tropical ecosystems can be considered as the "last unexplored frontier of the biosphere" where terrestrial arthropods constitute the most diverse group of eukaryotes. In this Ph.D. thesis, we used a set of complementary approaches (based on taxa, traits, evolutionary units) on assemblages of tropical spiders in systems with contrasting habitats to determine their diversity patterns and make inferences on the processes that locally drive them.

Due to the lack of knowledge on sampling and diversity of tropical spiders, we tested and compared different sampling methods (six) and standardized protocols by focusing on different strata. We developed a morpho-species database to overcome the lack of taxonomic knowledge. We studied a set of traits for spider assemblages to test their informative character in tropical environments. Finally, we determined evolutionary units to study diversity by applying a multilocus approach on a large collection of tropical spiders, assembled during this thesis, for which taxonomic knowledge is incomplete and problematic.

The main results of this thesis are summarized in Figure 1. These results are taken over and discussed together in the following paragraphs.

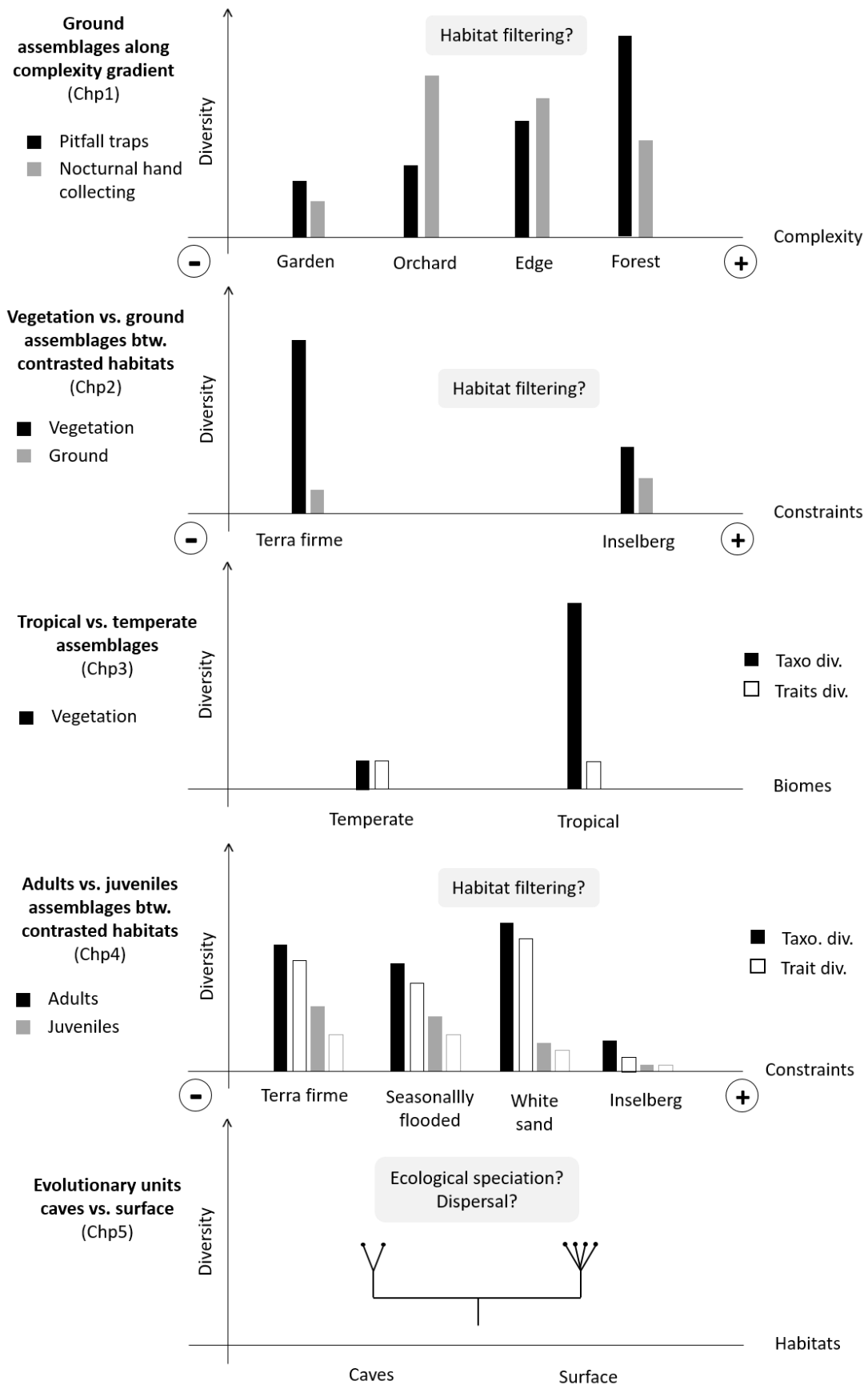


Figure 9: Synthetic view of the results obtained during this thesis illustrating the different habitats studied as well as the different compartments (e.g., strata, adultes or juveniles) of the spider assemblages

By comparing spider assemblages of habitats varying in complexity and constraints, we have shown that these habitats harbor different assemblages with contrasting taxa (Chapters 1, 2, and 4) and traits (Chapters 1 and 4) diversities. These results suggest the existence of environmental filtering on the tropical spider assemblages, as it has been showed for temperate spiders (e.g., Ridel et al., 2021) and another hyperdiverse taxon of arthropods in neotropical forests (e.g., ants Fichaux et al., 2019). However, these patterns do not always follow linearly the habitat gradients we identified (Chapters 1 and 4 when juveniles are considered), highlighting the need to investigate in detail the factors that influence the assemblages.

The correlation between taxon and trait diversity was also tested during this Ph.D. thesis. At local scales, trait diversity was following the same patterns as taxon diversity between contrasted tropical forests habitats (Chapter 4) but not between more open and disturbed habitats (Chapter 1, comparison between garden, orchard, edge and forests). These contrasting results are surprising as trait-based diversity is known to be correlated to taxonomic diversity as a rule, by mathematical effects (plants: Pavoine et al., 2013, spiders: Ridel et al., 2021). At a broader scale, the patterns of traits and taxon diversity were not correlated as the difference of taxonomic diversity between tropical and temperate assemblages was way higher than the one in trait diversity. This result echoes with Cardoso *et al.* (2011), which showed that trait diversity was not always higher in tropical regions compared to temperate regions, arguing for a higher trait redundancy of traits in tropical spider assemblages.

Focusing on evolutionary units, we showed that highly contrasted habitats (caves vs. surface) harbor different lineages, suggesting a strong environmental filter and ecological speciation (Chapter 5). When comparing evolutionary units from less contrasting habitats (different altitudes and climates at the surface), diversity patterns in evolutionary units were less clear, suggesting that environmental filtering is not driving diversity but that other factors, such as dispersal, influence diversity (Chapter 5).

The various studies conducted during this thesis thus highlight the **influence of habitats, and thus of the habitat filter, on the diversity in taxa, traits, and evolutionary units of tropical spider assemblages but suggest as well that taxonomic and trait might be driven by different environmental factors.**

Research perspectives

The interlinking of the approaches used during this Ph.D. thesis revealed new questions that should be addressed by future research.

Further investigations of the assembly rules of tropical spiders

Contextual and scale-dependent patterns of diversity

We looked at different systems with contrasting habitats: a garden-orchard-woodland-ridge-forest complexity gradient (Chapter 1), flooded forest-inselberg forest (Chapter 2), dryland forest-flooded forest-inselberg forest, and flooded forest-dryland-white sand forest (Chapter 4) constraint gradients, as well as cave vs. surface (Chapter 5). The differences in diversity patterns between these systems (Figure 1) show that, given our knowledge of tropical spider taxonomy, traits and phylogeny, diversity patterns are context-dependent.

Testing different sampling methods allowed us to study the diversity of different strata (i.e. soil vs. understory) and different compartments within a stratum. By comparing the diversity of spider assemblages in tropical floodplain forests and inselberg forests, we showed that ground assemblages were more diverse on inselbergs (Chapter 2) while understory assemblages were more diverse in tropical floodplain forests (Chapters 2 and 4) (see Figure 1). Russell-Smith & Stork (1994) showed that canopy assemblages were more diverse on inselbergs. Using different methods sampling the same stratum, we showed that diversity patterns vary within the same stratum for soil (Chapters 1 and 2) but not for vegetation (Chapters 2 and 4). Within the same stratum, microclimatic conditions can vary considerably and influence species distribution (Foelix 2010).

These variations in diversity patterns between and within strata suggest that there are abiotic conditions at very small scales, constituting micro-habitats for spiders and that these micro-habitats are important in structuring these tropical spider assemblages. A micro-habitat is a small area that differs from the surrounding habitat in terms of abiotic conditions such as vegetation structure and complexity, light exposure, or temperature (e.g., Entling *et al.* 2007). The importance of micro-habitats has been shown in other spider assemblages (e.g., Jiménez-Valverde & Lobo 2007, Corcuera *et al.* 2008, Foord *et al.* 2008, Ziesche & Roth 2008). It has been suggested that spider assemblages may be more diverse on a vertical plane than on a horizontal plane (i.e. than between habitats, Abraham 1983). This confirms what has been found elsewhere on the tropical arthropofauna as a whole, for which it has been shown that stratification in tropical vegetation does not follow the same laws as in temperate (Basset *et al.* 1992, 2003), with notably finer variations within the same stratum, potentially also linked to the fact that the known vertical gradient of temperate vegetation is not found in tropical (Basset *et al.* 2003). However, the critical factors determining this small-scale vertical

structuration of tropical spider assemblages need to be investigated at the same time as the habitat scale factors.

We note that no variability in diversity patterns (taxonomic diversity and composition) was detected during this thesis within the 'understorey' stratum (Chapters 2 and 4), which is surprising because the different sampling methods used targeted different strata of it: the lower stratum for mowing and the upper stratum for threshing (Scharff *et al.* 2003, Vedel & Lalagüe 2013), as well as the entire stratum for the Amazonas-trap (Lopes *et al.* 2019). It can be speculated that vertical structuring of understorey vegetation might be less important for these tropical spider assemblages than for other assemblages for which this parameter is crucial (e.g., Hansen *et al.* 2016, Gallé *et al.* 2017). However, the lack of variation we observed might also result be related to a finer structuring of this vegetation stratum (Basset *et al.* 2003).

Studying the phylogenetic units of Hawaiian wolf spiders, we showed that cave wolf spiders lineages might also be influenced by small-scale variations that could be limited by environment, resources, or dispersal (Chapter 5). Trophic segregation (Arnedo *et al.* 2007) and microhabitats influence (Gillespie *et al.* 1997, Eberle *et al.* 2018) are known to play a role in spider diversification and have to be investigated for these wolf spiders.

The variation in fine-scale diversity (microhabitats) that we have highlighted in this Ph.D. thesis, coupled with the presence of many singletons and the different stratification of tropical habitats and the finer distribution of arthropod assemblages within them (Basset *et al.* 1992, 2003) leads us to question the aggregation patterns of spiders in tropical environments. Coddington *et al.* (2009) reviewed the possible reasons for the over-representation of rare species ("singletons") in tropical assemblages and concluded that this is due to under-sampling. However, it is also possible that tropical spider faunas follow different aggregation patterns (Chao *et al.* 2009, Coddington *et al.* 2009) that we believe should be investigated in future research to fully understand the rules of tropical spider assemblages. We also propose that future research should address singletons by investigating whether their rarity based on abundance is also recovered by examining their rarity status based on their traits and phylogeny, i.e. by assessing their trait originality and phylogenetic originality (see Kondratyeva *et al.* 2019).

Environmental factors driving diversities

The context- and scale-dependent patterns of diversity, as well as the fact that taxonomic and trait diversities are not always correlated (and thus are driven by different environmental factors), emphasize the necessity to test which environmental factors determine the habitat filtering at those different scales and for the different components of diversity. There is an important literature on factors driving spider assemblages that we started to review in that sense (Entling *et al.* 2007, Overgaard *et al.* 2011, Prenter *et al.* 2012, Hansen, Hansen, Bowden, Normand, *et al.* 2016, Ameline *et al.* 2018), and some like vegetation structure, altitude and flooding will be evaluated in the coming work on the data from the Chapter 4.

Rethinking sampling in tropical environments: the need to use a set of sampling methods in standardized protocols

By testing several sampling methods commonly used in (temperate) spiders and parameters known to influence assemblages (e.g., day vs. night), we have shown that our knowledge on the use of sampling methods in temperate is not generalizable to tropical assemblages, even when applying standardized protocols (Chapters 1 and 2). Indeed, sampling intensities are insufficient to have a complete view of diversity (Chapters 1, 2, 3 and 4), methods supposed to sample the same assemblages show different efficiencies, sample different assemblages (for soil) and detect different diversity patterns (Chapters 1 and 2).

By comparing spider assemblages collected by methods known to target the same strata, we demonstrated that these different methods (1) collect different assemblages, in terms of diversity and taxon composition, (2) with different patterns of taxonomic diversity between habitats (Chapters 1 and 2). We have also shown that taking trait diversity into account in the evaluation of the efficiency of sampling methods allows the detection of methods that collect a greater trait diversity (linked to the different assemblages targeted by these methods) (Chapter 1). In addition, a newly developed method (i.e. Amazonas trap, Chapter 4) targeting the shrub layer of the "understory" vegetation, collects assemblages whose patterns of taxonomic and trait diversity seem similar to those of other more known and used methods (i.e. beating and sweeping, Chapter 2). To characterize and compare the assemblages of different habitats and to understand the factors that determine them, it is, therefore, necessary to use several methods that a priori sample the same stratum in quasi-optimal protocols (*sensu* Malumbres-Olarte *et al.*, 2017): that are standardized but that are not optimized for one habitat only.

Designing a universal sampling protocol for tropical forests is a goal that has been pursued for a long time (Coddington *et al.* 1991) but cannot yet be achieved due to the lack of data (Malumbres-Olarte *et al.* 2017). Also, it is necessary to continue to apply and test sampling methods and protocols in different tropical regions of the globe to accumulate data, both on taxonomic and trait diversity collected by these methods.

Furthermore, we consider new statistical methods for comparing diversities using standardized approaches based on sampling completeness (Chao *et al.* 2014, 2021, Hsieh *et al.* 2016) to be indispensable due to the undersampling of tropical spider assemblage (approximately 33%, Coddington *et al.* 2009). These methods seem to us a boon to, in the future, reanalyze data from previously published studies on tropical spider diversities and draw conclusions about the effectiveness of sampling methods.

Importance of taxonomy

The difficulties caused by the absence of described species or questionable descriptions, whether for the study of taxonomic diversity (Chapters 1, 2, 3, 4) or the study of evolutionary units (Chapter 5), remind us of the importance of a clear and up to date taxonomy in the understanding of diversity patterns. The use of parataxonomy shows its limits, in cases such as the Hawaiian wolf spiders (Chapter 5) where morphological conservatism is such that species boundaries (if they exist) are impossible to determine on a morphological basis without a complete revision of lineage members and information about evolutionary diversity.

The diversity of tropical spiders is such that the task of species description is monstrous and seems insurmountable, despite the activity of taxonomic arachnologists (Agnarsson *et al.* 2013, Jäger *et al.* 2021), due to the current context in which taxonomy is unattractive and unfunded (Engel *et al.* 2021). In the context of a hyperdiverse group such as tropical spiders, it, therefore, seems to us that molecular methods could be a particularly suitable aid to species delimitation. Thus, we encourage future research on tropical spiders to modernize their collecting practices to be able to use molecular tools (NGS, i.e. RADtags) to delimit and describe unknown species encountered (Ivanov *et al.* 2021, but see also Courtial *et al.* submitted, Appendix 4 for a simple COI investigation) and at best apply genomic methods to these collections (Card *et al.* 2021). We encourage this research to also use tools such as the portable MinION platform, which allows sequencing to be performed in isolated tropical conditions (Pomerantz *et al.* 2018, Krehenwinkel *et al.* 2019).

Towards the development of a trait-based approach adapted to tropical ecosystems

As mentioned in the introduction and shown in the different chapters of this thesis (Chapters 1, 3, and 4), knowledge on spider traits, and tropical spiders, in particular, is limited. The creation of the World Spider Trait Database should allow the accumulation of more knowledge about them. However, this database only accepts traits from described species (Lowe *et al.* 2020, Pekár, Wolff, *et al.* 2021), further reinforcing the importance and urgency of describing tropical spider species.

In Chapter 4, we measured a set of traits whose correlations with environmental variables will allow us to link them with potentially determining factors of assemblages. This exploration is laborious but necessary (e.g., Wong & Carmona 2021) and will allow a qualitative gain in the study of traits in tropical assemblages.

Finally, due to the high under-sampling inherent in tropical spider (and arthropod) assemblages in general (Coddington *et al.* 2009), under conditions of feasible sampling intensity, comparisons of diversity in tropical assemblages are only rigorous if they account for sampling completeness (Chao & Jost 2012, Chao *et al.* 2020). While a method for

estimating taxonomic diversity exists (Chao, Gotelli, *et al.* 2014, Hsieh *et al.* 2016), it has only recently been developed for trait diversity (Chao *et al.* 2021, used in Chapter 4).

Using NGS to resolve complicated evolutionary relationships

Resolving the phylogenetic relationships and the origin of the radiation of the Hawaiian wolf spiders will require (1) a more complete sampling of the archipelago (surface and caves) as well as a sampling of the Pacific and neighboring continents and (2) use of genome-wide approaches. In this sense, samples from all over the Pacific, coming from museum collections, have been gathered and partly sequenced during this thesis. They should be included in further analysis. Moreover, extensive surface and cave sampling from the Hawaiian archipelago was supposed to be conducted during this thesis but has been delayed due to the Covid-19 pandemic. This fieldwork should be conducted in Spring 2022. Additional study on the cave species is ongoing in collaboration with Dr. Megan Porter and Dr. Rebecca Chong, University of Hawai'i, Manoa who recently submitted an NSF proposal entitled "Collaborative Research: BEE: Bridging the space-time continuum to investigate how biodiversity scales across subterranean systems" on which I will be collaborating. In particular, we plan to characterize the anatomical features of the Hawaiian wolf spider's eyes modification and do population genomics on the different cave systems.

Conclusion

The interlinking of the approaches used during this Ph.D. thesis revealed the influence of habitat in the taxon-, traits- and evolutionary units diversity patterns of tropical spiders and consequently the importance of habitat filtering in tropical spider assemblages. In addition, we have shown the context-dependent and scale-dependent nature of diversity patterns in tropical spiders with variations of tropical spider assemblages at a finer scale than that of habitats. Overall, this plaid for more case studies studying tropical diversity patterns at the scale of strata, vegetation sub-structures, and micro-habitat conditions, for which we are suggesting research axes. We were also able to make proposals to improve the sampling of tropical spider assemblages which should help to get comparable data to draw up, in the near future, the outlines of a universal sampling protocol for tropical forests. Proposals were also made to improve investigating the evolutionary units of rapid diverging lineages of spiders. Nowadays, we are fortunate to have data-sharing tools (World Spider Catalog, World Spider Trait Database) as well as new analysis methods (statistics, sequencing), which will allow us to fill this knowledge gap in the coming years. Finally, this work reminds of the need to continue to develop taxonomic knowledge, to keep using the species as the basic unit of studies in community ecology.

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APPENDIX

APPENDIX.1

Towards establishment of a centralized spider traits database

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Abstract

A main goal of ecological and evolutionary biology is understanding and predicting interactions between populations and both abiotic and biotic environments, the spatial and temporal variation of these interactions, and the effects on population dynamics and performance. Trait-based approaches can help to model these interactions and generate a comprehensive understanding of ecosystem functioning. A central tool is the collation of databases that include species trait information. Such centralized databases have been set up for a number of organismal groups but is lacking for one of the most important groups of predators in terrestrial ecosystems – spiders. Here we promote the collation of an open spider traits database, integrated into the global Open Traits Network. We explore the current collation of spider data and cover the logistics of setting up a global database, including which traits to include, the source of data, how to input data, database governance, geographic cover, accessibility, quality control and how to make the database sustainable long-term. Finally, we explore the scope of research questions that could be investigated using a global spider traits database.

Key-words: Phenotypic traits, functional diversity, functional ecology, ecosystem functioning, evolutionary ecology, comparative analysis

Introduction

We are living in an age of large-scale assembly of digital information. The generation of large databases across scientific disciplines is now enabling the modeling of natural processes on an unprecedented scale. The development of the world wide web over the last three decades has aided the centralization of collated data and has enabled the storing and sharing of large amounts of data. Biology has truly arrived in the information age with the large-scale digitization of information and its central storage in online databases (e.g., GenBank, BOLD, Dryad). These databases have become the core of many recent research advances.

In ecology and evolutionary biology, the accessibility of large-scale genetic information reaches its true potential when linked with phenotypic and faunistic data. For instance, comparative studies of organismal traits among species or across space, time or habitat types, can reveal general patterns that help to predict changes in biodiversity and ecosystem functioning in a rapidly changing world (Krause et al. 2014; Madin et al. 2016b; Wright et al. 2017; Dudley et al. 2019; Mammola et al. 2019). However, the development of open databases for phenotypic data is lagging far behind. This not only limits progress in the life sciences, but also leads to inefficient duplication and impairs reproducibility of research. Major reasons for the slow and reluctant establishment of trait databases are the perceived difficulty to unify data and to standardize reporting methods. In contrast, for molecular data these challenges have been overcome, facilitating the rapid growth of molecular databases. Furthermore, the inclusion of new molecular data into such central databases is highly promoted. For example, final acceptance of a publication in many scientific journals is contingent on the submission of genetic data to a genetic database (e.g., GenBank).

Compared to genetic data, trait data are much harder to standardize across taxonomic groups due to different terminologies and methods used for their measurement and recording. Therefore, existing trait database projects are taxon-specific and often constrained to specific traits or geographic regions (e.g., Kattge et al. 2011; Homburg et al. 2014; Brun et al. 2017; Madin et al. 2016a; Oliveira et al. 2017; Parr et al. 2017). There are good reasons to continue with the assembly of taxon-specific trait databases as this approach offers the flexibility required to tailor the database to the need of the focus field (e.g., entomology, herpetology, botany, microbiology). The data deposited in different taxon-specific databases could be synthesized into a central node by the identification of common or equivalent traits that can be easily

translated into cross-taxon standards (Gallagher et al. 2020). Examples of such traits already in use in cross-taxon studies are body size, trophic niche, habitat preferences, and metabolic rates.

Hence, the building of taxon-specific trait databases can bring enormous benefits both for the specific field compiling the data (e.g., arachnology) as well as for cross-taxon analyses. Here, we propose to set up a community-based spider trait database (Arachnida: Araneae) and invite submissions of data from the arachnological community.

Spiders are a mega-diverse order of animals, with about 48,400 species currently identified (World Spider Catalog 2020), and one of the most dominant groups of invertebrate predators in terrestrial ecosystems (Turnbull 1973). They thus play a key role in ecosystem function worldwide, such as increasing crop performance by suppressing pest density (Michalko et al. 2019). Spiders are premier subjects to study fundamental biological mechanisms, such as sexual selection (Herberstein et al. 2013), the evolution of sociality (Lubin & Bilde 2007) and extended phenotypes (Blackledge et al. 2009), predator-prey interactions (Pekar & Toft 2015), community assembly (Birkhofer et al. 2017), and migration (Gillespie et al. 2012). They are also in the focus of the applied sciences, such as agro-ecology (pest control) (Uetz et al. 1999; Birkhofer et al. 2016; Michalko et al. 2019), material science (spider silk) (Wolff et al. 2017) and medical science (venom) (King & Hardy 2013).

General database benefits

Trait databases are particularly useful for comparative studies and studies on biodiversity and the function of ecological communities. Traditionally, such research relied on the primary collation of comparative data by laborious measurements in a large number of species and specimens or time-consuming gathering from print-literature. The widespread lack of access to primary or even derived data has not only contributed to the reproducibility crisis of science (Allison et al. 2018) but also led to an unnecessary redundancy in data acquisition, wasting time and money. Only recently has it become a common good scientific practice to make the raw data that underlie a study available to the scientific community. While this enhances transparency, it does not necessarily solve the problem of work redundancy as such datasets that are largely hidden in appendices, electronic supplemental material or on file servers instead of a central repository. The building of a commonly accepted trait database is a solution.

Having open access to a database of relevant trait data not only boosts comparative and ecological studies, but also allows researchers to undertake quick exploratory analyses to generate preliminary data that may be useful for project planning and funding justification in grant applications. Well populated databases also make it possible to detect knowledge gaps or geographical biases, which can be used to identify future areas of research.

Trait databases thus fill an important gap in the digitization and accessibility of biological knowledge and can become a powerful tool when linked with existing taxonomic (World Spider Catalog 2020), semantic (Spider Anatomy Ontology—SPD (Ramirez & Michalik 2019)), molecular (BOLD (Ratnasingham & Hebert 2007), Genbank (Benson et al. 2012), ArachnoServer (Pineda et al. 2018)) and faunistic (e.g., Atlas of the European Arachnids; Atlas of Living Australia; Araneae Spiders of Europe (Nentwig et al. 2020); Global Biodiversity Information Facility—GBIF) resources (See Table. 1 for current databases that include spider traits). Finally, a trait database can also serve as a central data repository to fulfil the requirements of data accessibility.

Tableau 1.—Examples of existing databases which include data for spiders (overview compiled in January 2020).

Name	Geographic range	Data types	Number of species included	Link
Genbank	Global	DNA sequences	12537	https://www.ncbi.nlm.nih.gov/genbank/
BOLD	Global	DNA barcodes	10552	http://www.boldsystems.org/
British Spider and Harvestman Recording Schemes	Britain	Distribution, ecology, habitat	713	http://srs.britishspiders.org.uk/
Czech spider database	Czech Republic	Distribution, habitat	896	https://www.arachnology.cz/rad/Araneae-1.html
GBIF (Global Biodiversity Information Facility)	Global	Occurrence records	50708	https://www.gbif.org/
World Spider Catalog	Global	Taxonomy, species distribution	48423	https://wsc.nmbe.ch/
ArachnoServer	Global	Toxin sequence, structure and biological activity	100	http://www.arachnoserver.org
Araneae Spiders of Europe	Europe	Distribution, morphology (body length, diagnostic illustrations), habitat	5210	https://araneae.nmbe.ch/
Global Species Database of Salticidae	Global	Distribution, morphology (diagnostic illustrations)	6990	http://www.salticidae.pl/
Jumping spiders (Arachnida: Araneae: Salticidae) of the world	Global	Distribution, morphology (diagnostic illustrations)	6149	https://www.jumping-spiders.com/
Spider Anatomy Ontology (SPD)	Global	Ontology of anatomical terms	NA	http://bioportal.bioontology.org/ontologies/SPD

Benefits of a spider traits database

Setting up a global trait database for spiders will elevate arachnology to the next level of biodiversity digitization: having open and better access to data will bring arachnology together and create stronger collaborative networks able to address a wide range of questions (as explored below). It will make global or large-scale studies possible within a fraction of the time and improve the statistical power of many analyses. A centralized database will also help to identify species' vulnerability and guide conservation decisions (Gonçalves-Souza et al. 2015). It can also help to inform taxonomic decisions since the database acts as a source of information about variability (e.g., geographic and morphological).

Beyond arachnology, a spider trait database will facilitate the inclusion of spiders in global multi-taxa studies and biomonitoring programs. The topical research area of biodiversity-ecosystem functioning relationships often utilizes metrics of functional diversity that are based on traits in crosstaxon studies. The collation of global data will also provide better information for outreach purposes. For example, the database could provide information

about local diversity of spiders, size comparisons or peculiar species that are accessible to local residents. A comprehensive understanding of the functional and ecological diversity of spiders, if adequately published for the general audience, can help to improve the public perception of spiders.

As existing trait database projects are largely family-focused and no such database yet exists for any arthropod order, the arachnological community could lead a frontier project for higher-level animal trait databasing. We think that arachnologists are in an excellent position to swiftly establish a spider trait database due to its outstanding achievement of digitization of all taxonomical literature (Nentwig et al. 2015) and the existence of a digital taxonomic standard, the World Spider Catalog (WSC) (2020), which makes possible the large-scale extraction of basic traits, such as area of distribution or body size (e.g., through text mining approaches), and their automatically updated taxonomic assignment (through a unique LSID identifier).

Logistics of a traits database

Some of the logistics of setting up a trait database require consensus on: trait definitions, the source of data, how to input data, database governance, geographic cover, accessibility, quality control, financial needs, and how to achieve the database's long-term sustainability. Below we propose principles that, in our view, will make a useful framework for a spider trait database.

Definition of traits.—One of the fundamental problems with collating traits in particular is the confusion and debate around the term “traits”, and in particular “functional traits” (Violle et al. 2007; Pey et al. 2014; Moretti et al. 2017; Brousseau et al. 2018; Wong et al. 2019). At their most basic form, all observable and quantifiable characters are traits. While some traits directly imply an ecological function (e.g., ‘habitat preference’ (Rusch et al. 2015)), for basic phenotypic data, such as body shape, the link to function is often not experimentally established and remains hypothetical. Furthermore, to be useful for a wide range of topics beyond functional ecology, a database should be flexible enough to accommodate a diversity of data types. For a spider trait database, we propose that the term ‘trait’ should thus be applied in a broad sense and include all observable and quantifiable characters on the level of individuals, populations or species, irrespective of our current assumptions on their functional role.

For a highly versatile database, we propose the inclusion of the following trait categories: (a) Ecological (e.g., (micro-) habitat preference, hunting mode), (b) Behavioral (e.g., stratum utilization, maternal care), (c) Morphological (e.g., body length, leg length), (d) Physiological (e.g., reproductive rate, resting metabolic rate, thermal limits) and (e) Biomechanical (e.g., running speed, silk strength). In the future, the database may also be expanded to include more categories.

Data types.—Another challenge is that the nature of traits can be diverse: traits can be quantified and described using data that are descriptive (e.g., Latin name of a prey item), categorical (e.g., web-builder, active hunter), ordinal (e.g., small, medium, large), interval (e.g., 1–3, 4–6), ratio (e.g., 10:100; 20:100), discrete (e.g., 1,2,3) or continuous (e.g., 1, 3.5, 7.2). There are many examples where qualitative information is sufficient in order to capture the traits, but problems arise when researchers apply different terminologies, definitions and categorizations for observations or characteristics. While common standards must be identified for each trait to ensure comparability (e.g., fixing units for numerical traits), the versatility of trait input can be maintained by a liberal trait definition with the accurate method (e.g., recording scheme) defined in the meta data, which permits the filtering for comparable data at the analysis stage (Jones et al. 2006). Another solution is to handle differently recorded trait data under separately defined traits.

The use of non-equivalent data types for some traits presents further difficulties. For instance, different authors report phenology, habitat preferences or prey type as binary or in frequencies. Furthermore, the state of some categorical traits might be ambiguous or context dependent. For instance, in many orb-web spiders (Araneidae), the adult males abandon webs, and some long-jawed orb-web spiders (Tetragnathidae) can be both web-building or free hunting. This problem can be solved by recording any categorical trait state as binary with the option to provide a frequency for each character state and a record of the sample size. Some traits are covarying, e.g., body length and leg length. This can be accounted for by linking trait records that are derived from the same object (i.e., specimen, individual or population).

Intraspecific variation.—The impact of intraspecific variation on comparative approaches has been widely demonstrated (Garamszegi & Møller 2010) and has also been recognized in community ecology (Bolnick et al. 2011). Some spider species, such as *Argiope bruennichi* (Scopoli, 1772) (Araneidae) have a wide distribution range and show an enormous variation in phenology, morphology and behavior depending on the geographical location (Krehenwinkel & Tautz 2013; Wolz et al. 2020). In such instances, a single trait record may not be representative for a species. The trait database can provide the opportunity to accommodate multiple records per species and attach relevant information about the record context (such as locality, date and developmental stage) in the metadata.

Taxonomic integrity.—A serious challenge for the maintenance of multi-species datasets is taxonomic changes. Fortunately, with the World Spider Catalog (2020), arachnology has a reliable and maintained source for changing taxonomic information. A key is the assignment of a unique identifier (the Life Species Identifier (LSID)), which is constant and can be used as a link between the spider trait database and the World Spider Catalog to automatically update the taxonomic information in the database. To make any changes traceable, we propose that species names originally used in uploaded datasets must be kept in the metadata.

Database governance and data upload.—The spider trait database will be a community-driven project, created and maintained by a team of 5–10 administrators and a webmaster. To upload data, the contributor must use a template that provides the structure for how the

data and attached metadata are reported. An annotated draft template can be found in the electronic supplemental material of this article (Supplemental materials Online at <http://dx.doi.org/10.1636/JoA-S-20-011.s1>). At this stage, any trait data can be sent to the corresponding authors of this paper using this template for its inclusion into a first version of the spider trait database. The database will be hosted by Masaryk University, Czech Republic, and curated by Stano Pekar's research team and collaborators.

Quality control.—Databases require some degree of curation in order to maintain their integrity. While some of the data checking can be automated (i.e., if all mandatory fields contain information and data types for traits are correct), we think that the content of submissions must be formally crosschecked and approved by an expert before it is published in the database. This may include a quick check, if the uploader is a known expert, if the data are of relevance for the database, if the data are accompanied by a citable publication that described the methods of data acquisition and that there are no obvious errors (e.g., false units and digits). The formation of an editorial board with experts for specific types of traits (e.g., behavior, morphology, habitat) will help to facilitate the described curation task.

Accessibility.—Following the principles of FAIRness and open science (Wilkinson et al. 2016) and facilitating its embedding in the Open Traits Network (Gallagher et al. 2020), we promote open accessibility of the spider trait database. This can be enabled by the use of the creative commons license CC-BY 4.0, which means that anyone will be able to download and use the data for their own research with the appropriate citation of the database.

Author attribution.—Authorship models and citation rules for database usage are matter of dispute at trait database meetings. The reason is that the processing and integration of data from thousands of sources makes it hard to define what makes a significant contribution that merits authorship and who must be named and cited according to the ethical norms of science and the CC-BY license (Gallagher et al. 2020). Here it can be useful to distinguish between the authors of the original data sources (i.e., the publication from which data were extracted to build a comparative dataset) and the authors of the data synthesis (i.e., researchers who collated the comparative data set and/or made the database accessible in a systematic manner). For practical reasons, we propose that only the latter merits authorship of the database.

Following the above standards of reproducibility and traceability, it will be a requirement to cite the original data sources (preferably with a DOI) in the database. However, among the research community there is no consensus about whether original sources of legacy data must be cited in a publication that uses data from the database, and this decision is often left to the users (Gallagher et al. 2020). On the other hand, it is commonly accepted that any outputs derived from the trait database will reference the database (the synthesis). In order to become citable, the database will be released alongside an article in a scientific journal that describes the database. For the spider trait database, it is aimed to publish its formal description in a major Open Access journal. After the release, the database will be continuously updated and

its content expanded. Major changes to its content and the author team will require the occasional publication of a new article under a changed version number of the database.

Additional challenges for a spider traits database

The first major challenge of creating a spider trait database stems from the huge diversity of spiders (48,400 described species and many yet to be discovered), largely preventing arachnologists from gathering traits for all of them. One solution to this problem is to integrate data from related species in the analysis step, in a careful and controlled manner, which is a widespread procedure in comparative analyses of invertebrates (e.g., Madin et al. 2016b).

Second, many ecological studies use “morphospecies”, where species identification is considered too difficult. If species names are lacking, the common standard that makes the data comparable is missing. We argue that the arbitrary definition of morphospecies cannot replace species identification by experts, e.g., by comparison with species descriptions and type material, and we do not promote the inclusion of trait data from morphospecies into the database. However, to avoid the exclusion of data from lesser known taxa, the database will allow the use of genus levels as a common standard (i.e., usage of the genus LSID, if species identities are unknown or yet to be described). It will be encouraged to specify voucher IDs and locations, if present, in the meta data, to enhance the tracing of species identifications.

Potential research that would become feasible with a spider traits database

Metacommunity, macroecology and biogeography.—At its most basic level, a traits database will help answer questions about how traits are geospatially distributed across taxa. Studies on how traits evolve or change at the community level in response to natural and historic change would also be facilitated. Having access to data relating to trait composition and body size will enable researchers to study the macroecological drivers of functional diversity at broad spatial and temporal scales (Cardoso et al. 2011). It will also enable the study of the relative contribution of environmental filtering, dispersal-related processes and competitive exclusion in determining spider assemblages and their functional diversity (Jimenez-Valverde et al. 2010; Carvalho & Cardoso 2014). How the mechanisms of environmental filtering influence community assembly along environmental gradients (e.g., climatic, altitudinal, latitudinal, structural) and by abiotic and biotic disturbances (e.g., floods, fire and biological invasions) can also be investigated by integrating data from the trait database with data from other online resources, such as climatic databases (Carvalho et al. 2020). The integration of vegetation biome data and climatic gradients allows for the testing of the relationship between vegetation, latitude and functional diversity of spider communities. Finally, the effects of urbanization on the expression or evolution of spider traits could be studied on a global scale (Lowe et al. 2018).

Evolution.—To date, trait-based research is a topic largely promoted within macroecology, and less recognized in comparative biology. However, the digitization of traits has

considerable potential for the fields of comparative, evolutionary and systematic biology. By linking phylogenomic data with trait data, fundamental evolutionary questions can be studied on a large taxonomic scale, such as the evolution of body size (Kuntner & Coddington 2019) and the extended phenotypes (Blackledge et al. 2009). It would also be interesting to examine connections between phylogenetic diversity and functional diversity and to test the ‘stable species hierarchy hypothesis’ in spiders, which predicts that trait variation is higher at the interspecific level than at the intraspecific level (Kazakou et al. 2014). Furthermore, testable ideas include whether diversification processes have been accompanied by expansions or shifts in trait space and how the evolution of different traits are correlated.

Ecology and ecosystem functioning.—Trait based research can help to understand how communities and ecosystems work by unraveling the interactions between species and their ecological roles. With a comprehensive spider trait database, it could be feasible to identify which traits are associated with specific habitat types, such as the ones found in caves, deserts or mountain summits. In combination with similar databases of other taxa, the traits affecting ecosystem functioning, those affected by ecosystem processes, and traits that are redundant could be identified. Also, functional traits that have a similar (or complementary) ecological function could be identified. From an applied perspective, understanding which traits contribute to high levels of pest control by spiders (“effect traits”, Rusch et al. 2015) and how this service may be supported by certain management practices (“response traits”, Birkhofer et al. 2014) is an important research field in agriculture and forestry. Questions of niche formation in a competitive setting could be addressed, for instance what are the traits that confer competitive advantages under different circumstances.

Conservation.—The proposed spider trait database can guide conservation decisions. By identifying species that exhibit a unique combination of traits, local conservation can guide efforts targeting these species (Birkhofer et al. 2017). Comparative studies can reveal traits that are associated with species’ extinction risk, resilience or the recolonization of restored areas, for instance using model species’ vulnerability to climate and habitat changes (Chichorro et al. 2019). Future threats to biodiversity from land-use change or intensification could become predictable, if we understood community responses from a trait perspective. Comparing both taxonomic and functional diversity responses to agricultural intensification provides an ideal framework to consider trade-offs and synergies between different conservation goals (Birkhofer et al. 2015). To understand which species are threatened by the pet trade, the database can identify the traits, such as size or color, that make a spider attractive to the buyer.

Outlook

This paper demonstrates how the arachnological community and biologists more broadly would benefit from a global spider traits database. We have discussed the challenges that the development of a comprehensive trait database brings for a megadiverse group such as spiders and have provided possible solutions for each problem. We suggest that establishing

the spider traits database is feasible, but will require major support, endorsement and input by the community. Following a fruitful workshop on 10th February 2019, at the 21st International Congress of Arachnology in Christchurch, New Zealand, an action group has formed that is currently working on the implementation of the principles discussed in this article. The team, led by Stano Pekar, is currently setting up the online database, with the release of a first version planned for the end of 2020. We are requesting both data submissions (using the provided template) and participation in editing, testing and data curation. For questions, suggestions and offers please contact the corresponding authors of this article.

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APPENDIX.2

The World Spider Trait database (WST): a centralized global open repository for curated data on spider traits

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Abstract

Spiders are a highly diversified group of arthropods which play an important role in terrestrial ecosystems as ubiquitous predators, making them a suitable group to test a variety of eco-evolutionary hypotheses. For this purpose, knowledge of a diverse range of species traits is required. Until now data on spider traits have been scattered across thousands of publications produced for over two centuries and written in diverse languages. To facilitate access to such data we developed an online database for archiving and accessing spider traits at a global scale. The database has been designed to accommodate a great variety of traits (e.g., ecological, behavioural, morphological) measured at individual, species or higher taxonomic levels. Records are accompanied by extensive metadata (e.g., location, method). The database is curated by an expert team, regularly updated and open to any user. A future goal of the growing database is to include all published and unpublished data on spider traits provided by experts worldwide and to facilitate broad cross-taxa assays in functional ecology and comparative biology.

Background & Summary

With almost 50,000 species described to date¹, spiders are among the most diverse orders of terrestrial arthropods². Spiders rank among the most dominant arthropod predators in a huge variety of ecosystems, and therefore provide important ecosystem services, such as biological control^{3,4} and bio-indication⁵. They are also potentially an important source of molecules to be used in new biotechnologies and human medicine^{6,7}. In addition to these uses, spiders provide suitable models to test a breadth of ecological and evolutionary hypotheses⁸⁻¹⁰.

Successful use of spiders for research and environmental assessments is based on knowledge of traits (morphological, ecological, physiological or behavioural characteristics) which characterise responses to environmental conditions and both change and define the effects of spiders on ecosystems functioning¹⁰. Assembling trait values for species in a community is laborious because for some traits and species this information either does not exist or is not easily available as it is hidden in old publications (often not in English), unpublished records, technical reports, or even field notes. Although difficult to access, the data available are extensive, as research on spiders has covered a huge diversity of topics for over 200 years¹¹. Data on spider traits continues to be generated on a daily basis, most of it being used in individual publications or retained in unpublished datasets. Trait data are stored in different places and forms, and most data that originated before the use of personal computers are only available from printed publications. More recently collected data are often stored in digital form in different repositories (from personal computers to data archive servers), but it is often difficult to compile and standardize datasets with different formats, and completeness of metadata, necessary for leveraging data for common purposes as pointed out in the concept of Essential Biodiversity Variables^{12,13}.

A single database that accommodates all trait data would enable scientists to investigate spiders more effectively and to perform large-scale comparative analyses¹⁴⁻²⁰. A trait-based approach has the advantage that some investigations (e.g., bio-indication) can be performed even when the taxonomic identity is missing or inaccurate (using morphospecies, for example)²¹. Using trait, instead of taxonomic information, also allows for a comparison of community patterns and responses across regions with different species pools²². For these purposes, it is important that trait data are available in appropriate quality and quantity, and have broad taxon and regional coverage. Overcoming these barriers will foster collaboration among arachnologists and other researchers that aim for multi-taxa analyses^{15,23,24}.

Trait databases already exist for a number of taxonomic groups, such as plants²⁵, fish²⁶, amphibians²⁷, corals²⁸, reptiles²⁹, copepods³⁰, butterflies³¹, and ground beetles³², with a similar aim to accumulate and organize available data in a single repository. The success of such databases can be seen in the frequent use by many scholars³³. A general database of spider traits has not yet been developed. However, a range of spider traits can currently be found in several online resources, for example, body size of European species³⁴, cytogenetic

data³⁵, protein toxins of spiders³⁶, habitat and phenology of British (<http://srs.britishspiders.org.uk/>) and Czech spiders (<http://arachnobaze.cz/>), and various traits of ground-dwelling spiders (<https://portail.betsi.cnrs.fr>).

Recently, Lowe et al.¹⁰ initiated the establishment of a centralized database that aims to cover all spider traits and store data in a single place under FAIR (findable, accessible, interoperable, reusable) principles³⁷. Lowe et al.¹⁰ built the foundation of such database by detailed coverage of the trait definition, their standardization, input data types, database governance, geographic cover, accessibility, quality control, and sustainability. Furthermore, Lowe et al.¹⁰ recognized that the unification of the trait records can only be accomplished by careful examination of the data during the validation procedure.

Following the initiative¹⁰ here we present a curated global database which follows the FAIR principles and hosts a variety of traits recorded for spiders (**Fig. 1**). With the potential to grow indefinitely, so far we have already collected data for more than 7,000 spider taxa. The database has two main goals: 1) to collect and curate trait data on spiders from different sources, either (un)published or to be published in the future; and 2) to provide public access to these data under a CC BY licence facilitating their widespread use by researchers.

Methods

Definitions

We adopted a broad definition of traits for inclusion to our database: any measurable phenotypic (i.e., morphological, ecological, physiological, behavioural, etc.) characteristic of an individual or taxon. This may also include ‘pure’ traits³⁸ as well as the response to environmental conditions or a treatment^{39,40}. Traits can be either quantitative (continuous, integers, proportions) or categorical (qualitative, binary, and ordinal). Trait values can represent individual-level measurements (single observation) to higher taxonomic (species-, genus-, family-) level measurements (aggregates), often recorded as a statistic (mean, median, minimum, maximum). We do not consider descriptive molecular data (such as DNA or protein sequences) or faunistic records to be traits unless these contain reference to some trait (e.g., habitat type), as these have already established repositories such as GenBank® or the Global Biodiversity Information Facility (GBIF).

The definition of specific traits (including units for numerical traits or eligible values for categorical traits) was adopted from widely used definitions in a variety of published papers on spiders. To achieve semantic interoperability each trait is described by standardized terms (Table S1). Two types of ontologies, describing the process of data collection and traits themselves, were implemented during development of the database structure as suggested by Kissling et al.¹². The process of measurement, i.e. details of data collection is provided as metadata and the trait measured is given in the main table (see below).

To increase the interoperability of this database with other databases, the next step in the update of the database will be setting up an expert team to develop ontologies, detailed

vocabularies, and hierarchical structure for all traits. Some traits thus might be re-defined. This will not affect the current content but will prepare space for a harmonised collection of future data.

Database structure

We developed an online application and architecture called World Spider Trait database, currently in version 1.0 (<https://spidertraits.sci.muni.cz/>), to store and retrieve trait data on spider species (**Fig. 2**). The database is able to accommodate traits measured at any taxonomic level. As many trait values show variation (phenotypic plasticity) as a response to varying conditions, each trait record can be accompanied by extensive metadata, describing the conditions under which it was measured (such as treatment, sampling method, geographic location, habitat, date). The database was built to meet the FAIR principles: it is available at a public domain under open-access licence in a machine-readable format. This is enhanced by comprehensive online search options, and export capabilities.

The database has multi-layered structure. It is composed of a main table (**Fig. 1**) including five mandatory variables, namely (1) Original species name (taxon name as reported in the original source), (2) Trait abbreviation (unique abbreviation of each trait), (3) Trait value (measured value of a trait), (4) Method abbreviation (unique abbreviation of each method used to measure a trait), and (5) Reference abbreviation (unique abbreviation of each source). Several other variables are optional, namely Measure (type of the measured value), Sex, Life stage (ontogenetic stage), Frequency (relative frequency of occurrence), Sample size (total number of observations per record), Treatment (treatment conditions), Location abbreviation (unique identifier of a location), Latitude, Longitude, Altitude, Locality (the name or description of the place), Country, Habitat (habitat type according to a local classification), Microhabitat, Date, Note (any note related to a record), Row link (unique identifier of related measurements), and Reference (full reference). For a detailed description of each variable and examples see **Table 1**.

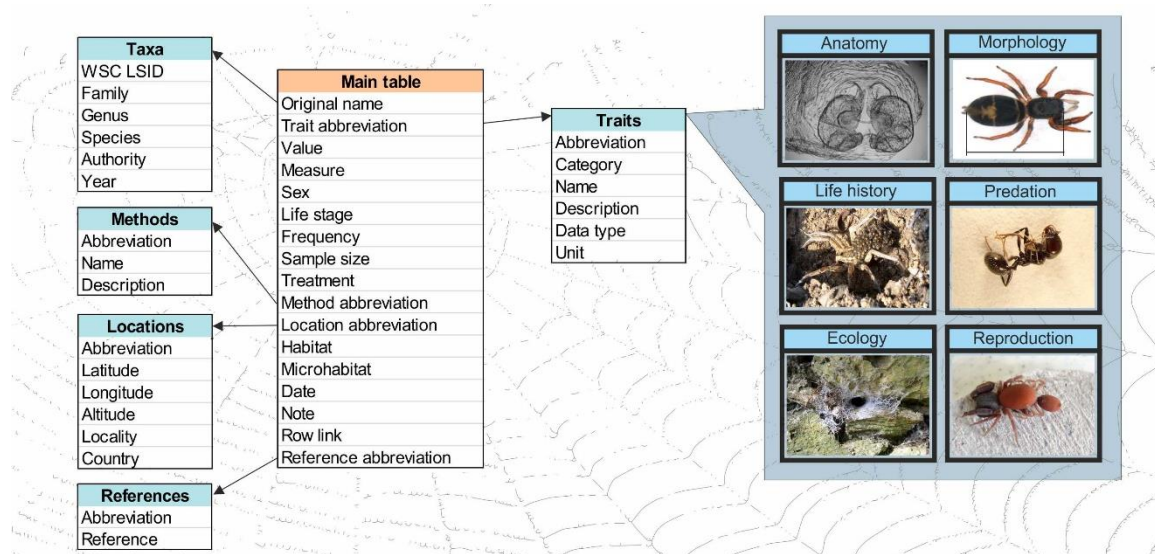


Fig. 1: A scheme of the database structure. There is the main table connected to five metadata tables. Examples of trait categories are given on the right. Photos: S. Pekár.

In the backend of the application, there are five additional metadata tables (extensions) which provide auxiliary information: (1) Taxa, (2) Locations, (3) Traits, (4) Methods, and (5) References. The Taxa table includes valid species or subspecies name, genus, family, LSID (Taxonomic identifier automatically retrieved from the World Spider Catalog¹), taxonomic authority and year. The content of this table is automatically updated on a weekly basis from the spider nomenclature information available in the World Spider Catalog¹, which contains valid Latin names and synonyms. Morpho-species do not have valid species names thus higher level categories (e.g., genus) are used optionally accompanied by additional information provided by the uploader in the Note variable. The Locations table includes country code, country name, locality name, coordinates, and its abbreviation. The Traits table contains Trait name, Category, Description, Data type, Unit, and its abbreviation. The Methods table includes method name, description and its abbreviation. References table includes full reference and its abbreviation. For more details see **Table 1**.

We defined 175 traits which are currently grouped into 13 categories according to the discipline (Anatomy; Biomechanics; Communication; Cytology; Defence; Ecology; Life-History; Morphology; Morphometry; Physiology; Predation; Reproduction) (**Table S1**). Information on the way a trait was measured is described in the Methods table. The provision of this metadata is mandatory during upload to ensure comparability of data. The Methods list includes field collection as well as laboratory methodology. Currently, there are 37 methods defined (**Table S2**). The included pre-defined traits, categories, and methods are meant to cover the majority of traits and methodologies in spider research; however, the architecture of the database is flexible enough that further traits, categories and methods can be added in the future, to accommodate new trait types and novel methodologies.

This database is hosted, developed, and maintained at the Department of Botany and Zoology of Masaryk University in collaboration with the University IT centre. It is connected to the World Spider Catalog¹, administered and curated by the core team members (**Fig. 2**).

Data upload procedure

Upon collection the data must be harmonised. Before a dataset can be submitted to the database, the data must be in a valid format (for a detailed description see <https://github.com/ookook/spider-trait-database/blob/master/docs/template.md>). For this purpose, we developed a MS Excel spreadsheet (Template) that should fit the great majority of trait types with predefined columns. The spreadsheet was designed to enable easy data manipulation by classical statistical software, such as R⁴¹. The template can be downloaded from the World Spider Trait database webpage (<https://spidertraits.sci.muni.cz/contribute>). It contains 31 columns, some of which are mandatory so they must be filled with appropriate numerical or character values. Eligible values for all columns can be found in the header of each variable, in the List of Traits (Table S1), and List of Methods (Table S2). If the input trait or method is not already defined the contributor should provide all of the following information to create a new trait or method: Trait category, trait name, trait description, trait data type, and trait unit in the case for missing

traits or method name and method description in the case of missing methods. Similarly, for references, the contributor either provides an abbreviation of a reference if it is in List of References or a full reference. Unpublished data are referenced as personal observations.

The data in the template then needs to be saved either as an .xls(x) or a comma-delimited.csv file and the file should be encoded as UTF-8 to assure compatibility with special (regional) characters. Once the template is uploaded the contributor must approve it using the tools within the web application.

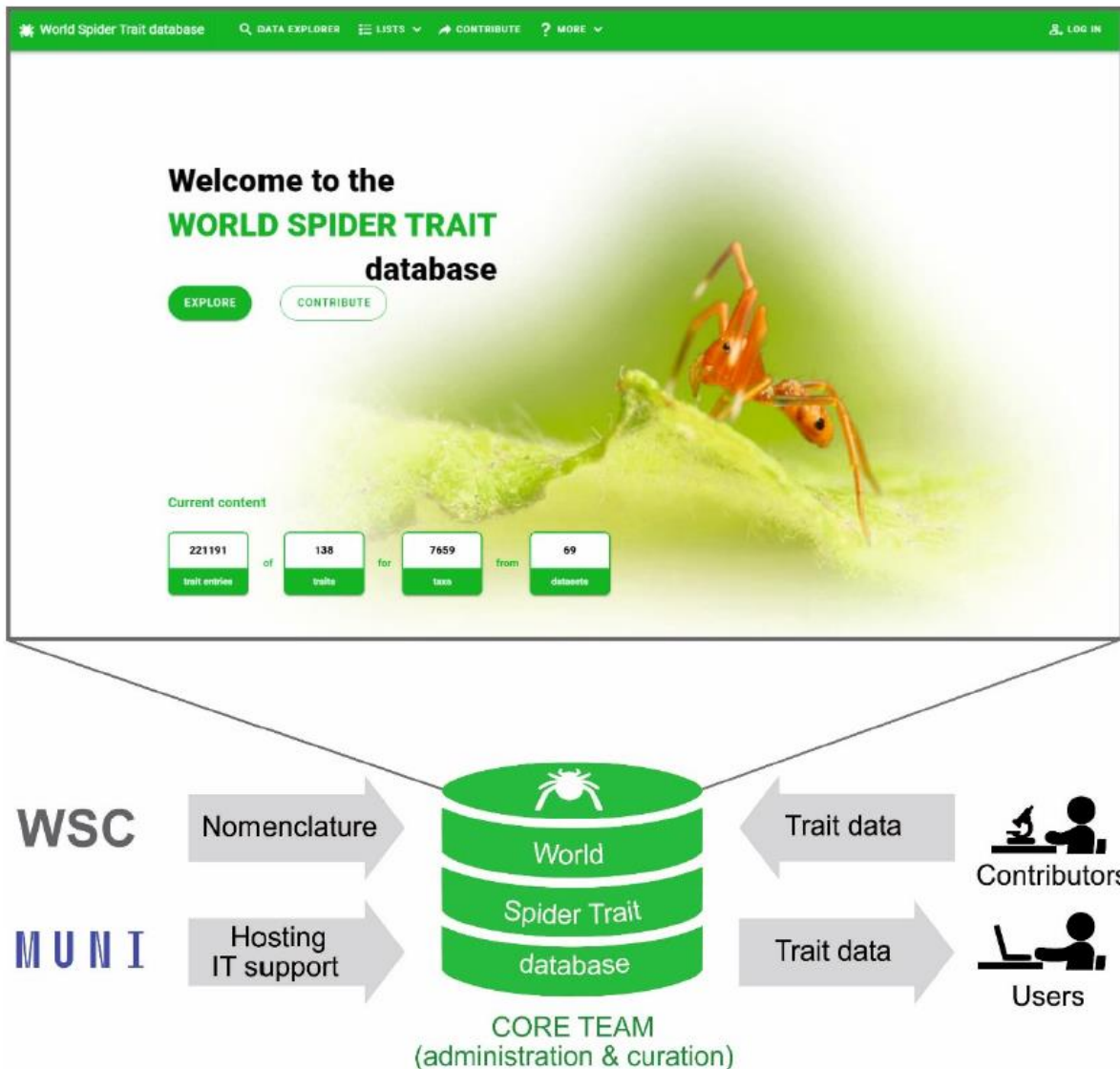


Fig. 2: The scheme of the World Spider Trait database application, depicting the role of contributing bodies and the frontpage of the webpage (<https://spidertraits.sci.muni.cz/>, accessed on March 5th, 2021). WSC stands for World Spider Catalog, MUNI stands for Masaryk University

Data Records

Integration of data from different sources was based on standardization and harmonisation. This involved conversion of trait values to comparable units/trait, use of controlled vocabulary in definition of traits, standardisation of eligible character values, and use of single spreadsheet format. Each record was accompanied by licence information and original source.

Currently, both published (from more than 1,000 publications) and unpublished data from diverse study designs (both descriptive and experimental) are included in the database with the citation of the original source⁴⁶. So far 70 datasets have been contributed with the total number of more than 221,000 records belonging to more than 7,500 taxa. Of these, 40 datasets (34.1% of records) are unlocked (i.e., freely accessible without registration). The remainder (i.e., embargoed datasets) are previously unpublished data compilations and can be viewed and downloaded by registered users only to ensure applicable authorship credits (see 'Usage Notes'). Registration and data usage is free under a CC BY licence. Embargoed data compilations may eventually become unlocked (e.g., once these have been used in published studies).

Geographical coverage of the database is global, but currently there are more records from Europe and South America than from other continents (**Fig. 3**)—a typical bias in biodiversity research⁴². Data on taxa from North America, Africa, and Asia are represented by very few records. The great majority of records available now come from Europe. Specifically, 20 datasets (66.1% of records) concern European species. This includes data on body size (2024 species), light & moisture preferences (1949 species), guild classification (1017 species), and conservation status (1557 species). In terms of traits, anatomical, behavioural, and physiological data are largely missing.

As for the taxonomic coverage, of 128 known spider families only two (Euctenizidae and Penestomidae) have no records in the database so far (**Fig. 4**). Several families (e.g., Gnaphosidae, Lycosidae, Salticidae, Sicariidae, Theridiidae) each have data for more than 40% of the 138 traits. But 38 families still have fewer than 5% of all traits covered. As for the number of records per family, most records come from the most speciose families, namely Linyphiidae, followed by Lycosidae, Theridiidae, and Salticidae (**Fig. 5A**). Because not every trait has been measured for every taxon, the taxon x trait matrix is highly incomplete (2.82% completeness, **Fig. 5B**). This is to be expected for a highly diverse and severely understudied taxonomic order. With respect to sex/stage, there are 33.6% records for adult males, 55.8% adult females, and 8.6 % for juveniles.



Fig. 3: Geographic coverage of the data in the database. Orange points represent geo-referenced records, while blue points are country centroids. There are records from 70 countries and 479 locations. The map was created using Google Maps.

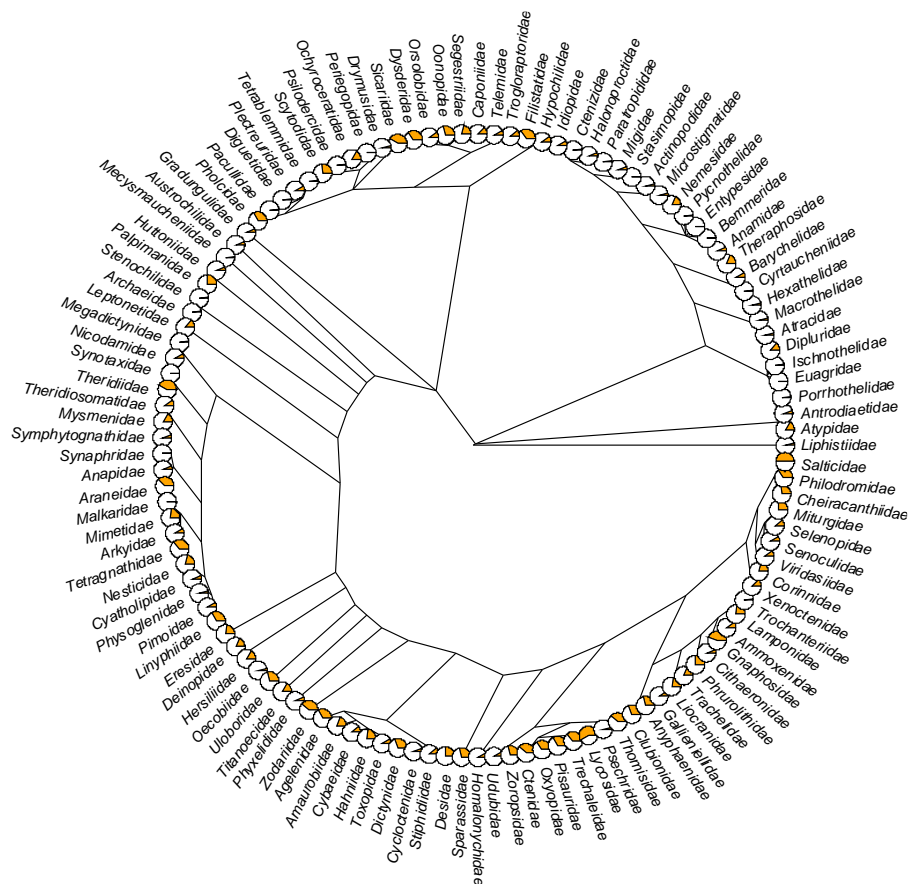


Fig. 4: Trait coverage mapped on the tree. The tree is on the family level (composed of 121 families which are represented in the database) with the proportion of the total number of traits (orange) displayed as pie charts (the fuller the pie the more traits). The tree was constructed based on the most recent phylogeny of spiders (Wheeler et al. 2017).

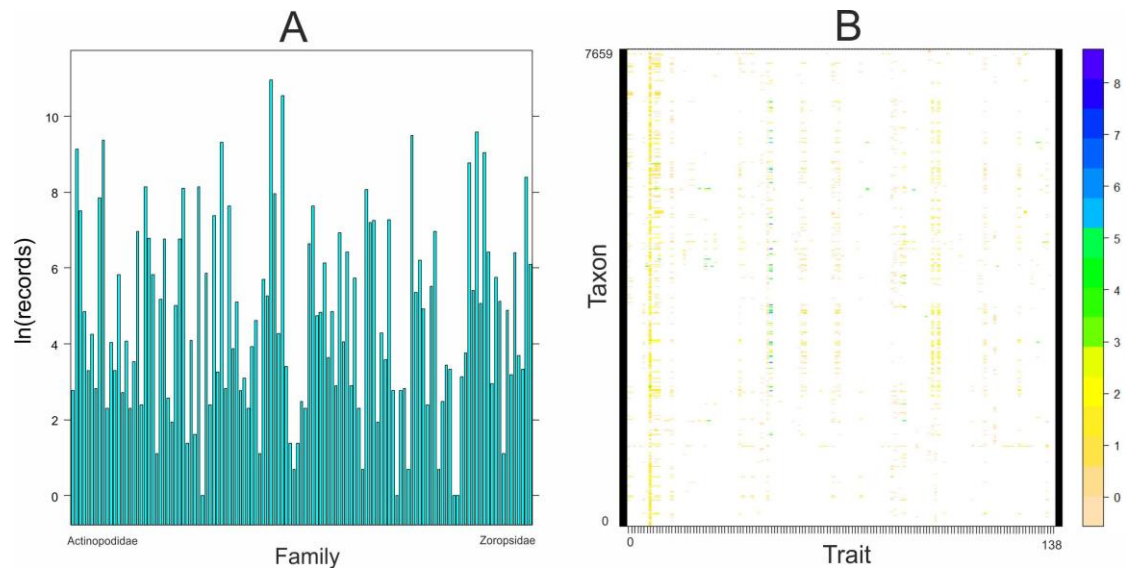


Fig. 5: Quantitative content of the database. A. Number of records (logarithmically transformed) for each family included in the database arranged alphabetically. B. The taxon by trait matrix representing the completeness. The most complete traits include body length (64% of taxa), followed by cephalothorax length (23%), and cephalothorax width (19%). Dots represent logarithmically transformed number of records per taxon. Taxon includes one of the following: subspecies, species, genus, or family.

The content of the database reflects real historic differences among geographic areas and disciplines. The database thus can be used to identify gaps and help to prioritise future areas for investigation to achieve more complete sets of records. To fill these gaps we plan to encourage contributions from specific areas, traits, and trait categories in the future. This can include collection of data from other repositories, extraction of data from publications, and archiving currently produced data. We will also ask curators of specialised spider trait databases to provide their data to be centrally stored here. Since many funders and journals now require data to be made publicly available, the database can be used as a permanent data archive option (an alternative to, e.g., Dryad or Figshare) provided that each contributed dataset meets standards of the database format which allows efficient reuse and synthesis. Each dataset obtains a unique URL and, in near future, it will be associated with a DOI provided by DataCite. In the future we expect to gather mainly data on new traits and new taxa and would like to encourage colleagues to contribute their datasets of both published and unpublished data. A coordinated effort is needed to achieve this goal.

To promote the process of data collection, we invite arachnologists to download the template and use it for data storage on their personal computers. At the same time, we ask arachnologists to get use to the vocabulary of the database, adopt definition of the traits that is used here (or suggest a different one) and develop protocols that follow the same standards. This will markedly enhance integration of their datasets with the database.

Technical Validation

Validation is performed at several steps during submission in order to retain only high quality records.

Firstly, a contributor is advised to search through the current database content in order to ensure that such (exact) data are not already included. It is also useful at this point to check whether the proposed trait(s) and method(s) are already defined. Contributors become eligible to upload their dataset after requesting registration from the administrator.

To upload a new dataset a contributor must specify the name of the dataset, their full name and email address. In addition, a contributor can specify authors of the dataset, author emails, mark whether the data can be immediately accessed or are under an embargo, and add any note. Then, the dataset sheet is created and the contributor is able to upload the data. The data is then imported to the temporary cache. During the upload process the web application checks the presence of eligible values in the following variables (Original name, Trait abbreviation, Value, Measure, Sex, Life stage, Frequency, Sample size, Method abbreviation, Latitude, Longitude, Altitude, Country, Date, Reference) and identifies duplicate records. Invalid records are highlighted to facilitate corrections. The taxonomy check includes existence of the name and match with a current valid name according to the World Spider Catalog¹.

At this stage, the contributor can view the dataset and must edit invalid cells in order to comply with the database requirements. Editing is done using the web application tools. When the contributor completes all changes and the dataset is valid, it can be sent to the administrator or editor for a review. The contributor can include a message to the editor when submitting the dataset for review in which the contributor can explain any problems the contributor had encountered while editing the dataset.

The administrator or editor is informed of a new dataset submission by an email. The dataset enters a second validation phase which can only be done by the administrator or editor. The administrator or editor must add new trait(s) and method(s) to the database, check for additional errors, such as extreme (unlikely) values of traits (e.g., resulting from typos, wrong digit separator, etc.), imprecise definition of new traits and methods, or an incorrect format of references. Once the dataset is validated by the administrator or editor it is published in the database. This means that all the data are transferred from the temporary import cache to the main database and becomes available to the general public. If the administrator or editor observes any problems, the dataset is rejected and sent back to the contributor with an email containing a description of the problem(s) to be fixed. Any dataset can be *post-hoc* corrected/alterred by the administrator or editor with/without contributors' consent.

Usage Notes

A user can view the whole content of the database using the Data Explorer within the online application. In the Data Explorer the user can apply filters (Family, Genus, Species, Original name, Trait category, Trait, Method, Location, Country, Dataset, References, Row links) to display selected content. The result can be displayed in a spreadsheet or in bar figure window. Selected data can then be downloaded in a .csv or .xlsx format. If the selected data contain data from datasets under embargo the user is given a warning. In order to download embargoed data the user has to send a request to the administrator or editor, who will then contact the dataset authors. All data with or without embargo can be download only after receiving login data.

In addition, the database provides an Application Programming Interface (API) to allow access to data via web platforms or software. An R package, named *spidR*⁴³, with few easy-to-use functions that allow downloading and pre-processing data from the database is now available. Resulting data frames can then be analysed with a variety of tools available in R⁴¹. Access of the embargoed data via API requires login as well.

As the trait value data can be a mixture of various statistics, it is important that the user checks the 'Measure' variable of each record and adopts appropriate procedures prior to analysis. Furthermore, due to inherent variation in most trait values, the user must consider conditions (such as habitat, altitude, treatment, etc.) under which it was measured. Not all conditions (e.g., hunger state, mating status, etc.) are recorded in the auxiliary variables, thus the user is strongly advised to study the original publication.

A number of traits included in this database are candidates of Essential Biodiversity Variables proposed by the Group on Earth Observations Biodiversity Observation Network^{12,13}. The traits are recorded with many metadata and thus allow quantification of intra-specific variation with respect to environmental conditions, space and time. These traits can be of societal relevance as they can be used in study spread of invasive species or biodiversity change.

Although the use of data is free, users are strongly encouraged to contribute their data particularly if they have not contributed yet following the simple 'first give, then take' principle. Only by these means the database will grow in quantity and frequency of use.

Contained data are publicly available under a Creative Commons Attribution license (CC BY 4.0), so that anyone can use received data under the condition of appropriate citation of this publication. In the case of datasets that have not been published and are under embargo, the user must agree with the dataset contributor on the conditions of use. Typically, this should include citation (URL or DOI) of the specific dataset in addition to the database citation.

Code Availability

The code of the web application is stored at GitHub (<https://github.com/ookook/spider-trait-database>) and is available under the GNU GPL v3.0. The phylogenetic tree was produced using functions within ape package⁴⁴ within R⁴¹.

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Supplementary information

Table S1: List of Traits, arranged alphabetically within trait categories.

Abbr.	Category / Name	Description	Data type	Unit	Eligible values
	<u>Anatomy</u>				
brsi	Brain size	Volume of CNS	real number	mm ³	
cuth	Cuticle thickness	Thickness of a cuticle on a body part	real number	mm	
nugl	Number of silk glands	Number of any silk glands per spinneret	integer		
prsy	Posterior respiratory system	type of posterior respiratory system (e.g., booklungs, tubular tracheae, lamella, absent)	character		
scle	Sclerotisation	Enhanced sclerotization of prosoma	character		
sigl	Silk gland size	Volume of any of the silk glands	real number	mm ³	
stfo	Sperm transfer form	State in which sperm is transferred to the female	character		
vgsi	Venom gland size	Volume of a venom gland	real number	mm ³	
	<u>Biomechanics</u>				
adhe	Web adhesion	Adhesion of capture thread	real number	MPa	
cspd	Climbing speed	Climbing speed (moving on a slope)	real number	cm/s	
rspd	Running speed	Running speed (moving horizontally)	real number	cm/s	
stra	Silk strain	Engineering strain of silk	real number	mm/mm	
stre	Silk strength	Engineering strength of silk	real number	Mpa	
toug	Silk toughness	Toughness of silk	real number	MPa	
	<u>Colouration</u>				
coop	Colouration of opisthosoma	Reflectance of dorsal side of opisthosoma at a certain wavelength (specify in Treatment variable)	real number	%	
copr	Colouration of prosoma	Reflectance of dorsal side of prosoma at a certain wavelength (specify in Treatment variable)	real number	%	
	<u>Cytology</u>				
chrn	Chromosome number	Diploid number of chromosomes	integer		

chrs	Sex chromosome system	The sex-chromosome system (e.g., XX0)	character		
chrt	Chromosome morphology	Type of chromosomes according to the position of the centromere (e.g., holocentric).	character		
	<u>Defense</u>				
modl	Model	Model imitated by species using camouflage and mimicry	character		Ant; beetle; wasp; snail; twig; branch; flower; etc.
prde	Primary defense	A strategy used prior to being detected by a predator	character		Cryptic (background matching); Cryptic (disruptive coloration); Cryptic (countershading); Aposematic; Batesian mimicry; Camouflage; Mullerian mimicry
pred	Predator	Taxonomical classification of a predator (e.g., wasp, bird, spider, etc.)	character		
retr	Retreat	Type of a retreat used to avoid predation	character		On web; in grass; under bark; silk sac; burrow; other
sede	Secondary defense	A strategy used after being detected by a predator	character		Death feigning; rapid escape; threatening posture; dazzle camouflage; startle; chemical deterrents; colour change; sound production
	<u>Ecology</u>				
balo	Ballooning	Occurrence of dispersal by ballooning (e.g., present)	character		
circ	Circadian activity	Hours of a day when the species is active (foraging, mating, web-building)	character		Diurnal; nocturnal; 1-24
disp	Dispersal time	Months at which dispersal occurs	character		January; February; March; April; May; June; July; August; September; October; November; December

girl	Global IUCN Red List category	Category of risk according to the global IUCN Red List guidelines	character		
habi	IUCN habitat	Habitat type according to the global IUCN classification	character		Forest; Savanna; Shrubland; Grassland; Wetlands; Rocky areas; Caves and Subterranean Habitats; Desert; Freshwater; Coastal; Urban, Agricultural; Other
halo	Habitat local CZ	Habitat type according to Czech habitat classification according to Chytrý M, Kučera T, Kočí M, Grulich V & Lustyk P. 2010. Habitat Catalogue of the Czech Republic. 2nd ed. Praha: Agentura ochrany přírody a krajiny ČR.	character		
lepr	Legal protection	Legal protection in national or subnational legislations	character		
ligh	Light	Light gradient according to Entling W, Schmidt MH, Bacher S, Brandl R & Nentwig W. 2007. Niche properties of Central European spiders: Shading, moisture and the evolution of the habitat niche. <i>Global Ecology and Biogeography</i> 16(4): 440–448.	real number		
lig2	Light 2	Light gradient according to Buchar J & Růžička V. 2002. Catalogue of spiders of the Czech Republic. Praha, Peres.	character		
mdl	Regional non-IUCN Red List category	Category of risk according to the regional guidelines (non-IUCN)	character		
miha	Microhabitat	Habitat where species occurs	character		among stones, bare ground, herbs, bushes, foliage, litter, etc.
moi1	Moisture 1	Moisture gradient according to Entling W, Schmidt MH, Bacher S, Brandl R & Nentwig W. 2007. Niche properties of Central European spiders: Shading, moisture and the evolution of the habitat niche. <i>Global Ecology and Biogeography</i> 16(4): 440–448.	real number		
moi2	Moisture 2	Moisture gradient according to Buchar J & Růžička V. 2002. Catalogue of spiders of the Czech Republic. Praha, Peres.	character		Dry, semi-humid. If possible give frequency (in field 'frequency'): 1 (preferred value), 0.5

					(primary value), 0.1 (marginal value)
ovws	Overwintering stage	Occurrence of overwintering (e.g., present)	character		
phen	Phenology	Months at which adult stage occurs	character		January; February; March; April; May; June; July; August; September; October; November; December
rasi	Range size	Area of the species distribution range	real number	km ²	
regl	Regional IUCN Red List category	Category of risk according to the regional IUCN guidelines	character		
soci	Social degree	Degree of sociality	character		Solitary, subsocial, colonial, quasisocial, social
strt	Stratum	Horizontal stratum occupied	character		Underground; ground; herb layer; shrub layer; tree trunks; canopy; wall
suaf	Subterranean affinity	Degree of subterranean affinity	character		Troglobiont, troglophile
	<u>Life History</u>				
indu	instar duration	Number of days spent in a certain ontogenetic stage (egg, larva, or instar) at a certain temperature (specified in Treatment variable)	integer	days	
inst	Number of instars	Total number of instars, beginning with the first free instar and ending with the adult stage	integer		
lonv	Longevity	Number of days from hatching to death	integer	days	
mort	Mortality	Mortality either natural or due to any treatment	real number	%	
sexr	Sex ratio	Number of males divided by the number of females	real number		
surv	Survival	Proportion of surviving individuals	real number	%	
	<u>Morphology</u>				
alsl	Spinneret ALS	Total length of anterior lateral spinneret (from base to tip)	real number	mm	
crib	Cribellum	Presence of functional cribellum and calamistrum (e.g., present)	character		
ente	Entelegyne	Presence of epigyne in females (e.g., present)			

eyes	Eye number	Total number of eyes	integer		
flat	Body flattening	Significantly flattened body as an adaptation to shelter in crevices	character		
nusp	Spine number	Number of erectable spines (macrosetae) on the prolateral side of leg I (that play a role in the formation of the capture basket)	integer		
scoa	Scopula area	Area of scopula hairs on leg segments	real number	mm ²	
scod	Scopula density	Number of scopula hairs per area on a leg segment	real number	mm ²	
spin	Spinnerets	Total number of functional spinnerets	integer		
	<u>Morphometry</u>				
abhe	Abdomen height	Opisthosoma height at highest point	real number	mm	
able	Abdomen length	Opisthosoma length from anterior to posterior along longitudinal axis (excl. petiole and spinnerets)	real number	mm	
abwi	Abdomen width	Opisthosoma width at widest point	real number	mm	
aled	ALE	Diameter of one anterior lateral eye	real number	mm	
alsl	Spinneret ALS	Total length of anterior lateral spinneret (from base to tip)	real number	mm	
amed	AME	Diameter of one anterior median eye	real number	mm	
bodm	Body mass	Body mass (in a normal nutritional condition)	real number	g	
bole	Body length	Total body length (from carapace frontal, excl. chelicerae, to opisthosoma posterior, excl. spinnerets)	real number	mm	
cehe	Cephalothorax height	Height of prosoma at the highest point (from sternum most ventral to carapace most dorsal)	real number	mm	
cele	Cephalothorax length	Length of prosoma (carapace) along the longitudinal body axis	real number	mm	
cewe	Cephalothorax width	Width of prosoma (carapace) at the widest point	real number	mm	
chle	Chelicerae basal part (paturon) length	Length of cheliceral base segment (paturon) along external margin	real number	mm	
cox1	Coxa I length	Coxa length of leg I	real number	mm	
cox2	Coxa II length	Coxa length of leg II	real number	mm	
cox3	Coxa III length	Coxa length of leg III	real number	mm	
cox4	Coxa IV length	Coxa length of leg IV	real number	mm	
criw	Cribellum width	Width of cribellum or colulus	real number	mm	

ctar	Claw tuft area	Projected area of adhesive foot pad (claw tuft) on leg IV	real number	mm ²	
ctde	Claw tuft density	Density of adhesive foot pad (claw tuft) on leg IV, i.e. number of tenent setae per area unit	integer		
eggs	Egg size	Diameter of an egg	real number	mm	
eggv	Egg volume	Volume of an egg	real number	mm ³	
epaw	Epigyne anterior plate width	Width of anterior border of epigyne plate	real number	mm	
epcw	Epigyne central plate width	Width of central border of epigyne plate	real number	mm	
eple	Epigyne length	Length of epigynal plate	real number	mm	
eppw	Epigyne posterior plate width	Width of posterior border of epigyne plate	real number	mm	
eyew	Eye region width	maximum width of eye region	real number	mm	
fale	Fang length	Cheliceral fang length from base articulation to the tip (measured along the median arc)	real number	mm	
fem1	Femur I length	Femur length of leg I (measured between condyles)	real number	mm	
fem2	Femur II length	Femur length of leg II (measured between condyles)	real number	mm	
fem3	Femur III length	Femur length of leg III (measured between condyles)	real number	mm	
fem4	Femur IV length	Femur length of leg IV (measured between condyles)	real number	mm	
l1le	Leg I length	Total length of one leg from the first (front) leg pair, excluding coxa and trochanter	real number	mm	
l2le	Leg II length	Total length of one leg from the second leg pair, excluding coxa and trochanter	real number	mm	
l3le	Leg III length	Total length of one leg from the third leg pair, excluding coxa and trochanter	real number	mm	
l4le	Leg IV length	Total length of one leg from the fourth leg pair, excluding coxa and trochanter	real number	mm	
met1	Metatarsus I length	Metatarsus length of leg I (measured between condyles)	real number	mm	
met2	Metatarsus II length	Metatarsus length of leg II (measured between condyles)	real number	mm	
met3	Metatarsus III length	Metatarsus length of leg III (measured between condyles)	real number	mm	
met4	Metatarsus IV length	Metatarsus length of leg IV (measured between condyles)	real number	mm	

ocdi	Ocular distance	Sum of diameters of one side of the caparace eyes (1 ALE, 1 PLE, 1 PME, 1 AME)	real number	mm	
pat1	Patella I length	Patella length of leg I (measured between condyles)	real number	mm	
pat2	Patella II length	Patella length of leg II (measured between condyles)	real number	mm	
pat3	Patella III length	Patella length of leg III (measured between condyles)	real number	mm	
pat4	Patella IV length	Patella length of leg IV (measured between condyles)	real number	mm	
pled	PLE	Diameter of one posterior median eye	real number	mm	
plsl	Spinneret PLS	Total length of posterior lateral spinneret (from base to tip)	real number	mm	
pmed	PME	Diameter of one posterior lateral eye	real number	mm	
pmsl	Spinneret PMS	Total length of posterior median spinneret (from base to tip)	real number	mm	
ptal	Palpal tarsus length	Length of palpal tarsus in males	real number	mm	
ptwi	Palpal tarsus width	Width of male palpal tarsus	real number	mm	
scoc	Scopula cover	Relative area of the prolateral side of leg I segment(s) covered with hairy adhesive pad (scopula, excluding claw tufts)	real number	mm ²	
stle	Sternum length	Width of sternum at widest point	real number	mm	
stwi	Sternum width	Length of sternum along the longitudinal axis	real number	mm	
tale	Tegular apophysis length	Length of tegular apophysis on male bulbus	real number	mm	
tar1	Tarsus I length	Tarsus length of leg I (measured between condyles)	real number	mm	
tar2	Tarsus II length	Tarsus length of leg II (measured between condyles)	real number	mm	
tar3	Tarsus III length	Tarsus length of leg III (measured between condyles)	real number	mm	
tar4	Tarsus IV length	Tarsus length of leg IV (measured between condyles)	real number	mm	
tawi	Tegular apophysis width	Width of tegular apophysis on male bulbus	real number	mm	
tib1	Tibia I length	Tibia length of leg I (measured between condyles)	real number	mm	
tib2	Tibia II length	Tibia length of leg II (measured between condyles)	real number	mm	
tib3	Tibia III length	Tibia length of leg III (measured between condyles)	real number	mm	
tib4	Tibia IV length	Tibia length of leg IV (measured between condyles)	real number	mm	
tro1	Trochanter I length	Trochanter length of leg I (measured between condyles)	real number	mm	
tro2	Trochanter II length	Trochanter length of leg II (measured between condyles)	real number	mm	
tro3	Trochanter III length	Trochanter length of leg III (measured between condyles)	real number	mm	
tro4	Trochanter IV length	Trochanter length of leg IV (measured between condyles)	real number	mm	

	Physiology				
gluc	Glucose content	Amount of glucose in a wet mass	real number	µg/mg	
ld50	Venom toxicity	LD50 of venom on <i>Drosophila</i> prey	real number	nl venom/ mg fly	
pydr	Drought tolerance	Relative humidity the spider can tolerate	real number	%	
pytl	Lower thermal limit	Temperature limit at which growth occurs	real number	°C	
pymr	Resting metabolic rate	Oxygen consumption per time when inactive	real number	W	
pysb	Submerging time	Time of surviving under water	real number	h	
pytu	Upper thermal limit	Temperature limit at which growth occurs	real number	°C	
prot	Protein content	Amount of proteins in a wet mass	real number	µg/mg	
trig	Triglyceride content	Amount of triglycerides in a wet body mass	real number	µg/mg	
	Predation				
cons	Consumption time	Time spent consuming certain prey (specified in Treatment variable)	real number	h	
guil	Hunting guild	Ecological hunting guild according to Cardoso P, Pekár S, Jocqué R & Coddington JA 2011. Global patterns of guild composition and functional diversity of spiders. <i>PLoS One</i> 6(6): e21710.	character		Sensing web weavers; sheet web weavers; space web weavers; orb web weavers; specialists; ambush hunters; ground hunters; other hunters.
klep	Kleptoparasitism	Occurrence of kleptoparasitism (e.g., present)	character		
nich	Trophic niche breadth	Levin's standardised index of niche breadth according to Hurlbert SH 1978. The measurement of niche overlap and some relatives. <i>Ecology</i> 59(1): 67-77.	real number		
para	Paralysis latency	Time between attack and prey immobilisation	real number	min	
prdi	Prey diversity	Shannon-Weaver index of diversity of captured prey as a measure of niche breadth	real number		
prek	Overkilling	Proportion of prey items killed but not consumed	real number	%	
prec	Prey capture	Mode of prey capture	character		Bite-and-release; grab-and-hold; wrapping; throwing silk; other

prem	Satiation	Number of prey items killed and consumed per certain time interval (specified in Treatment variable)	integer		
preo	Prey order	Taxonomic order of an organism the spider preys on	character		
prey	Prey	Type of organism the spider preys on (e.g., egg, caterpillar, imago)	character		
prsi	Prey size	Prey size (total body length)	real number	mm	
stsp	Strike speed	Time to complete a predatory strike (start of strike to first bite)	real number		
weba	Web area	Size of web projected in a 2-dimensional space	real number	cm ²	
webb	Web building	Use of a web for prey capture (not a retreat) (e.g., present)	character		
webd	Web diameter	Linear dimension of a web	real number	cm	
webt	Web type	Type of capture web	character		Orb web; cob web with gumfoot lines; sheet web; canopy web; space web; open tube; tube with trap door; tube with signaling lines; single line; other
webv	Web volume	3-dimensional size of a web	real number	cm ³	
	<u>Reproduction</u>				
coco	Coersive copulation	Presence of coercive mating indicated by causing injuries to the other sex (present, absent)	character		
codi	Cocoon diameter	Maximum diameter of the cocoon	real number		
coty	Courtship type	Sensual modality used during courtship (verbal description)	character		
codu	Courtship duration	Time from starting the courtship to the beginning of copulation	real number	min	
duma	Duration of mating	Total mating time	real number	min	
eggm	Eggsac mass	Weight of an eggsac	real number	g	
eggn	Number of eggs/sac	Number of eggs in a clutch (eggsac) / eggsac order	integer		
egsn	Number of eggsacs	Total number of eggsacs produced by a female during her life	integer		
eplu	Epigyne plugging	Mode of blocking access to the female epigyne	character		Excretion; embolus; none; other
fert	Fertility	Number of hatched offspring	integer		

maca	Maternal care	Extent of maternal care	character		None; guarding egg sac; guarding egg sac and spiderlings
maph	Matriphagy	Presence of matriphagy (i.e., offspring consuming tissue of their mother) (e.g., present)	character		
mapo	Mating position	Type of a mating position (e.g., type 1, 2, 3) according to Foelix R F. 2011. Biology of Spiders. 3rd ed. New York: Oxford University Press.	character		
nuin	No. of insertions	Total number of insertions during copulation	integer		
nupa	No. of partners	Total number of mated partners	integer		
ovip	Oviposition	Time to oviposition (following the first mating)	real number	days	
sexc	Sexual cannibalism	Occurrence of sexual cannibalism and the sex of cannibal (e.g., present/female)	character		
	<u>Sound</u>				
fred	Dominant frequency	The peak frequency of the sound produced	real number	Hz	
freq	Lower frequency range	The minimum frequency of the sound produced	real number	Hz	
freu	Upper frequency range	The maximum frequency of the sound produced	real number	Hz	
soun	Sound production	Mechanism of sound production (e.g., stridulation)	character		
sour	Sound source	Organ used to produce sound (e.g. chelicera and pedipalp)	character		

Table S5: List of Methods. For each method there is an abbreviation, name and short description.

Abbreviation	Method name	Description
bea	Beating	Capture by beating over net
cit	Citizen Science	Observation collected through citizen science
col	Colorimetry	Concentration assessment of a chemical compound in a homogenate
dis	Dissection	
exp	Expert-Base	Assessed based on expert opinion
fie	Field Observation	Observation performed in nature
fot	Photoeclector trapping	Capture by photoeclector
fun	Functional Response	Experiment of functional response
gut	Gut-Content Analysis	Molecular analysis of gut content
han	Hand Collection	Capture by individual hand sampling
kar	Karyology	Karyology on dissected tissue
lab	Laboratory Observation	Observation performed under laboratory conditions
mal	Malaise Trapping	Capture by Malaise traps
mic	Microscopic Measurement	Measurement done under microscope or in micro-photographs
mor	Morphometry	Length determination based on microscopy
mov	Movement Measurement	Measurements done using video-tracking software (e.g., Ethovision)
mul	Multiple data analysis	Analysis of results of former multiple studies
na	Not available	This information is not available
olf	Oloactometry	Measurement done using olfactometer
pan	Yellow Pan Trapping	Capture by yellow pan traps
pho	Photographic Analysis	Analysis of photographs
pro	Protein content	Measurement of protein content using Bradford's method
ptf	Pitfall Trapping	Capture by pitfall traps
res	Respirometry	Measurement done using respirometer
she	Shelter Trapping	Capture by shelters (e.g. bark bands)
sie	Sieving	Capture by sieving
sou	Sound Recording	Sound recorded by a recorder
spe	Spectrophotometric Measurement	Measurement done using spectrophotometer
suc	Suction trapping	Capture by a suction trap placed in the air
swe	Sweeping	Capture by sweeping net

tem	Transmission electron microscopy	Transmission electron microscopy using standard protocol for chemically fixed samples
the	Thermometry	Measurement done using temperature controlled chamber
tox	Toxicology	Toxicology bioassays
vac	G-VAC sampling	Capture by sucking up device.
ven	Venom potency test	Test of venom potency using a standardized protocol (specified in trait or notes)
web	Web Analysis	Analysis of the web content
wei	Weighing	Weighing on a lab scale (i.e. analytical balance)

APPENDIX.3

New species of *Hypaeus* Simon (Araneae: Salticidae: Salticinae: Amycini) based on integrative taxonomy

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Abstract

A new species of *Hypaeus* Simon is described from French Guiana based on both sexes, *Hypaeus olympeae* **sp. nov.** We employed morphological evidence, field observation, as well as the mitochondrial COI rapidly evolving loci to confirm that both males and females belongs to the same species. Finally, nine species are newly added to the list of salticids from French Guiana and 12 COI sequences corresponding to four so far unsequenced *Hypaeus* species are added to GenBank.

Key-words: Jumping spiders, Barcoding, Cytochrome C Oxydase Subunit 1, Taxonomy, French Guiana

Introduction

Neotropical spider's taxonomy is scarce (Scharff *et al.* 2003), partly because spiders are really diverse in neotropical forests (Cardoso *et al.* 2011; Privet & Pétilon 2018) and the human and material costs needed for their study are high; but this scarcity is also due to the huge proportions of rare species and juveniles in tropical assemblages (Coddington *et al.* 2009) and the difficulty to describe species based on only one specimen and therefore on a single sex and on juveniles. Spiders are a model group for ecological studies (Birkhofer & Wolters 2012; Cardoso *et al.* 2011; Malumbres-Olarte *et al.* 2018; Moya-Laraño *et al.* 2013) and the only group to be exclusively predatory among the dominant terrestrial arthropods (Birkhofer & Wolters 2012; Pekár & Toft 2015). Improving their taxonomy is thus crucial to understand neotropical diversity and ecology.

Within the neotropical forests of the Amazon, the most abundant and speciose spiders are the jumping-spiders (Salticidae; Bodner & Maddison 2012) and the richest subfamily is Amycinae (Araújo & Ruiz 2015; Maddison 2015). Among them, *Hypaeus* Simon 1900 may be one of the richest genera with 28 described species distributed from south to central America (World Spider Catalog 2021).

Species of *Hypaeus* are morphologically recognizable from their high carapaces, plumose setae over front eyes, pluridentate chelicerae with 4-5 teeth on promargin and 3-6 on retromargin, mastidia on male chelicerae and third leg longer than fourth (Galiano, 1968; Ruiz & Madisson 2015). However, *Hypaeus* is still poorly sampled and described and the boundaries of the genus are not completely understood (Araújo & Ruiz 2015).

Galiano (1963, 1968) redescribed and revised 18 *Hypaeus* species described by Crane (1943), Mello-Leitão (1948), Peckham & Peckham (1885), Simon (1900) and Taczanowski (1871, 1878). She also transferred two species to this genus, *Amycus mystacalis* (Taczanowski, 1878) and *Triptolemus benignus* (Peckham & Peckham, 1885); and synonymized one, *Mago budoninus* (Caporiacco, 1954). Two others were described by Crane, *H. duodentatus* Crane, 1943, and by Caporiacco, *H. barromachadoi* Caporiacco, 1947. Recently, the male and the female of the type species of the genus *Hypaeus*, *H. taczanowskyii* (Mello-Leitao, 1948), were redescribed by Araújo & Ruiz (2015). The same authors added four new species to the genus, *H. tridactylus*, *H. famoratus*, *H. poseidon* and *H. terramediae* Araújo & Ruiz 2015, and transferred *Hasarius pauciaculeis* (Caporiacco, 1947) to *Hypaeus*. The last issue from Martinez & Galvis (2017) added three new species, *H. arhuaco*, *H. proszynskii* and *H. varzea* Martinez & Galvis, 2017. Of the resulting 28 *Hypaeus* species, 17 have been described only from males (Araújo & Ruiz 2015; Martinez & Galvis 2017; World Spider Catalog 2019).

Methods such as the combination of morphology with DNA barcoding should help to overtake the limitations of tropical spider's taxonomy linked to juveniles and rarity. Phylogenetic analyses are also needed to resolve the relationships within this genus (Ruiz *et al.* 2019). However, only sequences for two *Hypaeus* species, *H. mystacalis* (Taczanowski, 1878) and *H. miles* (Simon, 1900), are available to date.

One hundred and two species of Salticidae are currently listed for French Guiana (Courtial *et al.* 2014; Vedel *et al.* 2013) and among them three *Hypaeus* species: *H. flavipes* (Simon, 1900), *H. porcatus* (Taczanowski, 1871) and *H. taczanowskii* (Mello-Leitao, 1948). During our last expeditions conducted in French Guiana (see Privet *et al.* 2018; Privet & Petillon 2018), in the National Nature Reserves of La Trinité and Les Nouragues, we collected numerous species of Salticidae and among them several specimens of the genus *Hypaeus*; this includes a species new to science. In this study, we used a combination of morphology and DNA barcoding targeting COI to match and describe the male and female from a new species, *Hypaeus olympeae* **sp. nov.**, produce sequences for four other *Hypaeus* species never sequenced so far, and add nine species to the list of salticids from French Guiana.

Material and Method

Taxon sampling

Taxa included in this study are 12 individuals of salticids belonging to the genus *Hypaeus*. They were collected in La Trinité (4°35'20"N; 53°18'1"W) and Les Nouragues (4°04'18"N; 52°43'57"W) Nature Reserves (French Guiana) during two surveys conducted in 2010 and 2013 (see Privet *et al.* 2018; Privet & Petillon 2018). In these reserves, seasonally flooded (Aya and Pararé) and summit inselberg (La Roche Bénitier and Nouragues) forests were sampled. Inselbergs are rocky outcrops rising abruptly from the surrounding landscape where little research has been devoted to invertebrates, especially spiders (Privet *et al.* 2018). The 12 specimens were morphologically identified; 6 accessions were assigned to *H. taczanowskii* and 4 to *H. porcatus*. Two specimens, impossible to assign to any of the currently recognized *Hypaeus* species, correspond to the new species described here, *Hypaeus olympeae* **sp. nov.** Total DNA of the 12 *Hypaeus* specimens was then extracted using non-destructive method (see below).

Specimens

The type material examined is deposited at the Muséum national d'Histoire naturelle (MNHN, Paris). Preserved specimens were studied using an OlympusSZX9 stereomicroscope with a Moticam5 (5.0MP) camera. Living holotype male and paratype female were photographed with a Canon EOS 450 D digital reflex camera with a 60 mm macro lens. The epigyne was macerated in 10% KOH. The specimens were preserved in 70% ethanol. In order to make easier comparison between *Hypaeus* spp. recently described by Araújo & Ruiz (2015), measurements (in millimeters) were taken according to Edwards (2004). The following abbreviations are used:

AME = anterior median eyes

co = copulation opening

dg = digital gland

eb = embolus base

et = embolus tip

po = pocket

sp = spermathecae

ta = tibial apophysis

RNN = Réserve Naturelle Nationale (National Nature Reserve)

MNHN = Muséum national d'Histoire naturelle, Paris.

The drawings of male individuals of Galiano (1963, 1968), Crane (1943), Ruiz & Brescovit (2008), Araujo & Ruiz (2015) and Martinez & Galvis (2017), as well as the reviewing of type specimens stored at the MNHN (Paris, France), allowed us to identify the new species *Hypaeus olympeae* **sp. nov.** collected in French Guiana.

DNA extraction, amplification, sequencing and data assembly

DNA was extracted using DNeasy 96 Blood and Tissue Kit (Qiagen) following manufacturer's recommendations. The entire specimens were directly placed in lysis buffer with proteinase K overnight to extract DNA without compromising morphological requirements for further examination (Paquin & Vink 2009). The standard animal DNA barcode fragment of the mitochondrial cytochrome-c-oxidase subunit 1 (COI) was targeted by PCR using the primers C1-J-1718 "SPID" (Simon *et al.* 1994) and C1-N-2776 (Hedin & Maddison 2001). PCR reactions were performed in 25 μ L and contained 0.5X PCR Buffer, 0.2 mM dNTPs, 1 mM MgCl₂, 0.15 μ M of each primer, 0.02 U/ μ L of Taq polymerase (GoTaq, Promega) and 2 μ L of DNA. PCR amplification started with an initial 94°C denaturation step for 2 min, followed by 35 cycles of (i) denaturation at 94°C for 45 s, (ii) annealing at 50°C for 45 s, and (iii) extension at 72°C for 60 s; a final 72°C extension step lasted 10 min. Sequencing of PCR products was performed by Genoscreen (Lille, France) using the same primers than for amplification. Sequence fragments were imported, assembled and edited in Geneious 6.1.8 (Biomatters Ltd., Auckland, New Zealand). All sequences, with voucher information, are archived in GenBank (Table 1).

Phylogenetic analysis

The taxonomic sampling used for the phylogenetic analyses included the 12 sequences newly generated for the study as well as one GenBank accession of *Sarinda cutleri* (Richman, 1965) (JX145669), a closely related species (see Maddison *et al.* 2014) that served as outgroup. All sequences were aligned in Geneious using MAFFT v.7.017 (Katoh & Standley 2013).

The resulting COI matrix was subjected both to Bayesian inference (BI) and maximum likelihood (ML) analyses. We first searched for the best-fitting nucleotide substitution model using the Akaike information criterion (AIC) estimated by MrModeltest v.2.3 (Nylander 2004); the GTR + G model was selected and assigned to all following phylogenetic analyses. The software MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) and RaxML-HPC v.8.1.24 (Stamatakis 2014) implemented on the CIPRES Science Gateway (Miller *et al.* 2010) platform were used to perform BI and ML analyses, respectively. MrBayes analyses constituted two independent parallel runs of four Markov chains each, implemented for one million generations and

sampled every 100 generations. Adequate mixing of the Markov chains and convergence of the two runs were confirmed with Tracer v1.6 (Rambaut *et al.* 2014). After removing a 10% burnin, the remaining trees were used to generate a 50% Bayesian majority-rule consensus tree. For the RaxML analyses, node support was assessed using a rapid bootstrapping algorithm with 1000 bootstrap iterations.

Table 1 : Summary of GenBank accession numbers, species name and voucher information (site coordinates are given in the Material and Methods) for the sequences newly generated for the study. [INFORMATION INTENDED FOR THE REVIEW PROCESS ONLY: The sequences generated for the present study are in the process of being submitted to GenBank. Once the GenBank accession numbers for all these sequences have been generated, we will update the table].

GenBank accessions	Name in topology	Voucher	Collection location	Sex
x	<i>Hypaeus olympeae</i> 1	ACAV07 3	La Trinité, French Guyana	♂
x	<i>Hypaeus olympeae</i> 2	ACAV07 2	La Trinité, French Guyana	♀
x	<i>Hypaeus porcatus</i> 1	NPTN11	Nourages, French Guyana	♀
x	<i>Hypaeus porcatus</i> 2	AQJ5	La Trinité, French Guyana	♀
x	<i>Hypaeus porcatus</i> 3	AQN1	La Trinité, French Guyana	♂
x	<i>Hypaeus porcatus</i> 4	AQJ5	La Trinité, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 1	NITJ3	Nouragues, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 2	NIQN9	Nouragues, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 3	IQN10	Nouragues, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 4	NPQJ7	Nouragues, French Guyana	♀
x	<i>Hypaeus taczanowskii</i> 5	PQJ4	Nouragues, French Guyana	♀
x	<i>Hypaeus taczanowskii</i> 6	NPQJ5	Nouragues, French Guyana	♀

Results

Class Arachnida Cuvier, 1812

Order Araneae Clerck, 1757

Family Salticidae Blackwall, 1841

Subfamily Salticinae Blackwall, 1841

Tribe Amycini F.O Pickard-Cambridge, 1900

Genus *Hypaeus* Simon, 1900

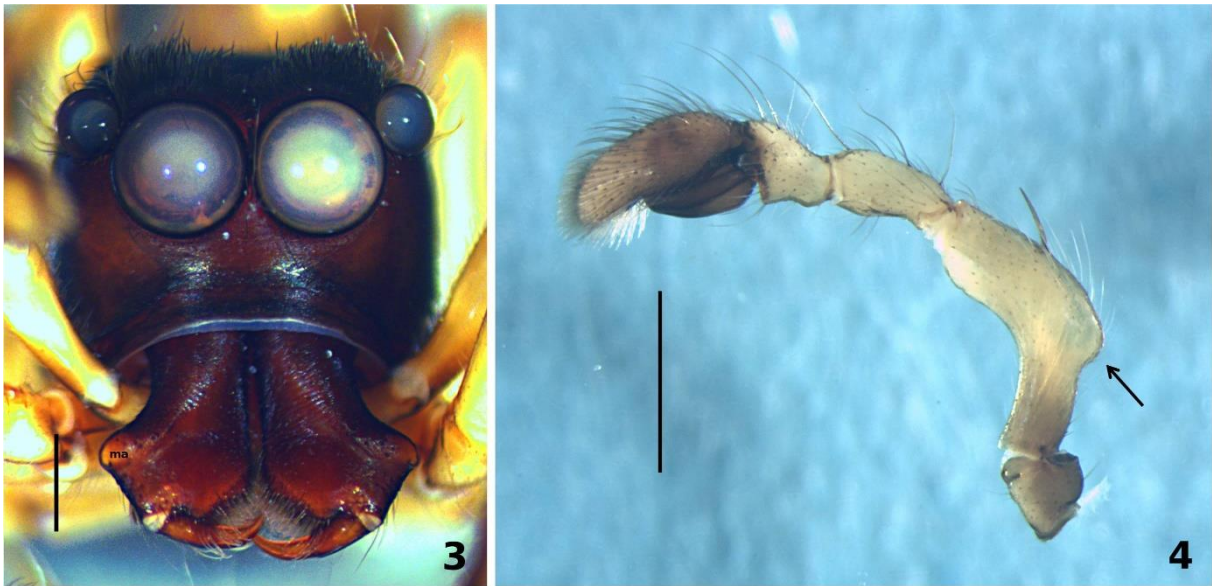
Hypaeus Simon, 1900: type species *Acragas taczanowskii* Mello-Leitão, 1948.

***Hypaeus olympeae* Courtial & Picard sp. nov.**



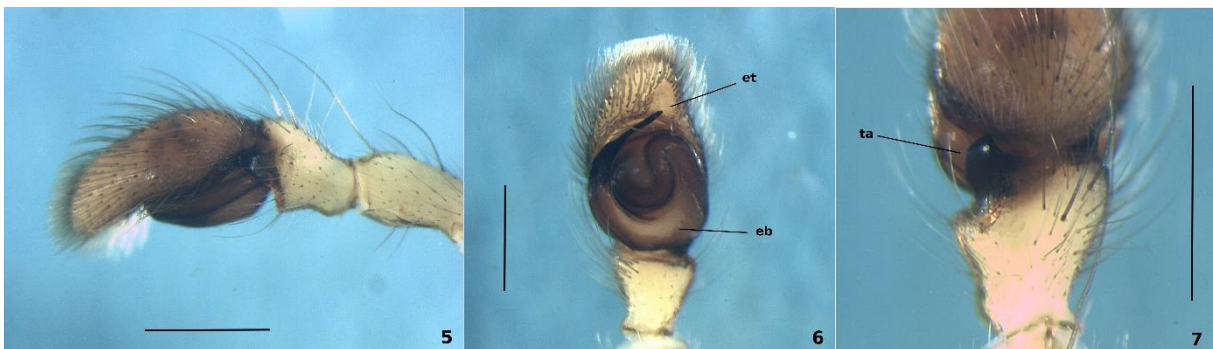
Figures 1 – 2

Hypaeus olympeae sp. nov. 1 male, dorsal view, scale 0,5mm; 2. Female, dorsale view, scale 1mm.



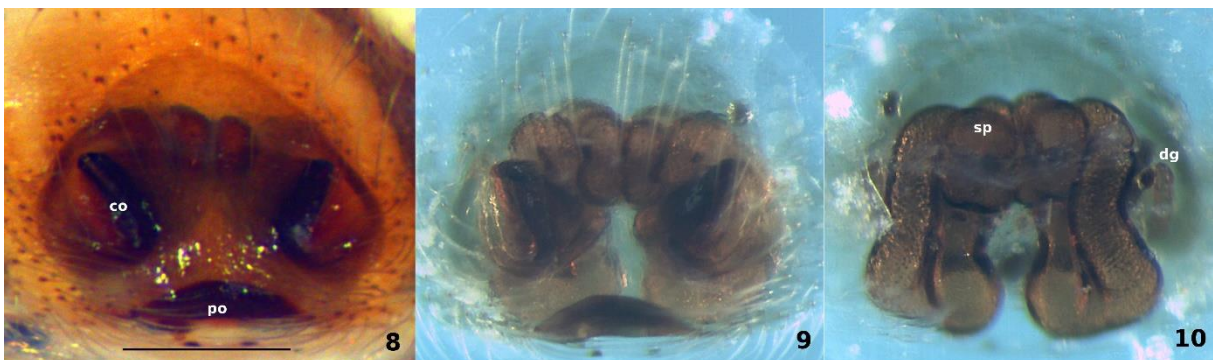
Figures 3 – 4

Hypaeus olympeae **sp. nov.** male. 3. Chelicerae detail (ma: mastidion), scale 0,5mm; 4. Left male palp with bump on femur (arrow), scale 1mm.



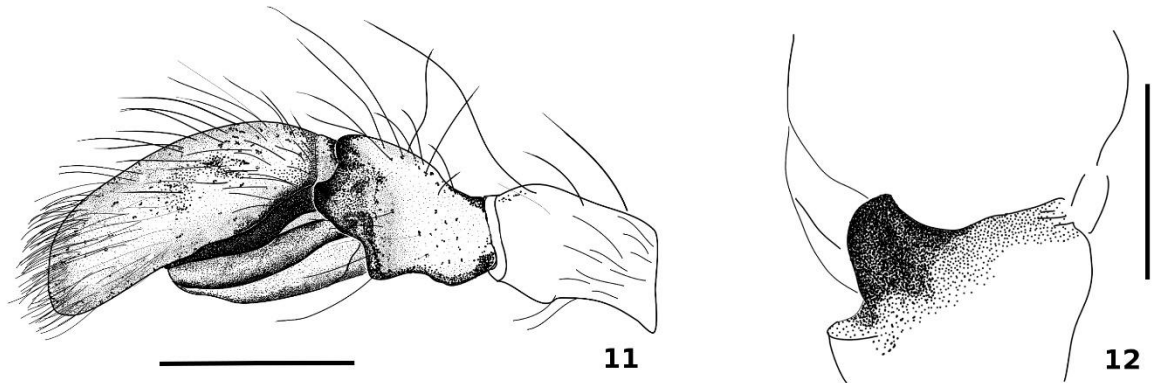
Figures 5 – 7

Hypaeus olympeae **sp. nov.** left male palp; 5. retrolateral view; 6. Same ventral view; 7. Same dorsal view showing tibial apophysis, scale 0,5mm.



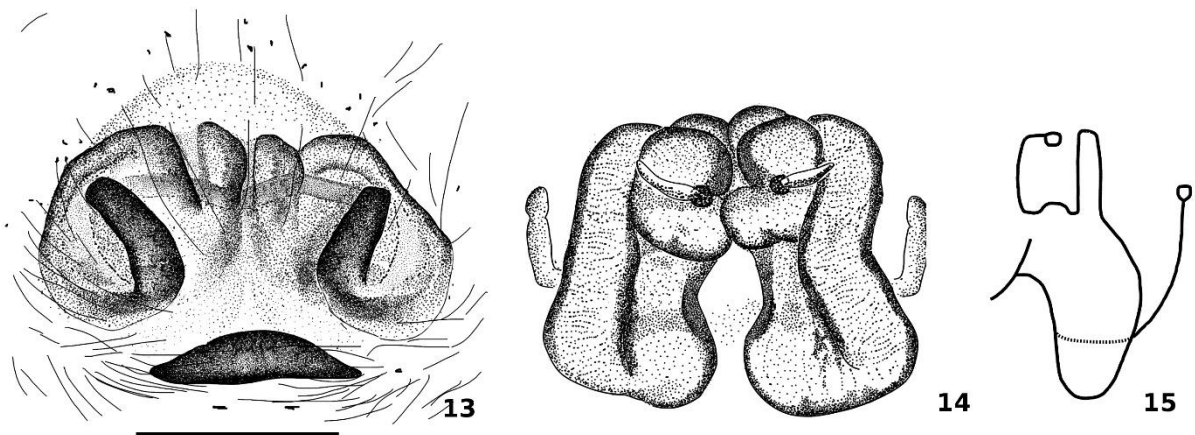
Figures 8 – 10

Hypaeus olympeae **sp. nov.** female; 8. epigyne, ventral view; 9. same, cleared; 9. ventral view, cleared, scale 0,5mm.



Figures 11 – 12

Hypaeus olympeae **sp. nov.** left male palp drawings; 11. retrolateral view; 12. same, dorsal view showing tibial apophysis, scale 0,5mm.



Figures 13 – 15

Hypaeus olympeae **sp. nov.** female; 13. Epigyne drawing; 14. same ventral view; 15. path within epigyne, scale 0,5mm.



Figures 16 - 17

Hypaeus olympeae **sp. nov.** pictures of alive specimens; 16. male holotype; 17. female paratype.

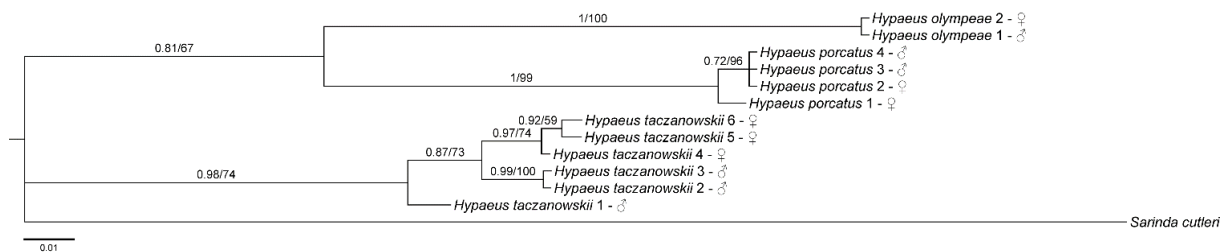


Figure 18

50% majority-rule tree from the Bayesian analysis of the COI matrix. Numbers above each branch are bootstrap values > 50% followed by posterior probabilities from the Bayesian analysis. Branch lengths are proportional to the number of substitutions per nucleotide position (scale bar=0.01 substitutions). See Table 1 for complete voucher information.

Differential diagnosis

Males of *Hypaeus olympeae* **sp. nov.** are similar to those of *H. miles* Simon, *H. femoratus* Araújo & Ruiz and *H. terraemediae* Araújo & Ruiz for having dilated femora (Fig 4). However, *H. olympeae* **sp. nov.** has wider rounded TA, with one is small and pointed in *H. miles*, *H. femoratus* and *H. terraemediae*. Females of *H. olympeae* **sp. nov.** are similar to those of *H. femoratus* and *H. terraemediae* (the female of *H. miles* is unknown). Digitiform glands curve from the center of the epigyne to the anterio lateral portion. Females of *H. olympeae* **sp. nov.** are slightly similar in shape to those of *H. femoratus* and *H. terraemediae* but the copulation openings are less curved and space between them is bigger.

Etymology

The species is named *olympae* to pay tribute to Olympe Delavalle, daughter of the Curator of the NNR Nouragues during our survey.

Material examined

Holotype

Male from RNN des Nouragues (4°02'N, 52°41'W), Camp Pararé, French Guiana, 11.XII.2013, Cyril Courtial (AR 16169).

Paratypes

One female from RNN des Nouragues (4°02'N, 52°41'W), Camp Pararé, French Guiana, 11.XII.2013, Cyril Courtial (AR 16170); one male, two females from RNN de la Trinité (04°36'N, 53°24'W), Camp Aya, French Guiana, 08.XII.2010, Alain Canard.

Additional material examined

French Guiana. RNN de la Trinité, Camp Aya (04°36'N, 53°24'W): 1♂, 01.XI.2008, Frédéric Ysnel ; RNN des Nouragues, Camp Inselberg (4°05'N, 52°41'W): 1♀, 09.XII.2013, Cyril Courtial ; RNN des Nouragues, Camp Pararé (4°02'N, 52°41'W): 1♀, 26.VI.2010, Vincent Vedel ; Montagne des Chevaux (4 43'N, 52 24'W): 1♀, 09.XI.2010, Vincent Vedel ; Roche Bénitier (04°36'N, 53°24'W) : 1♀, 06.IV.2010, Vincent Vedel.

Description

Male (Holotype, AR 16169)

Total length: 6.00. Carapace dark brown with light spot behind the fovea bearing white setae (Fig 1), 3.10 long, 2.30 wide, 1.80 high. Occular quadrangle 2.00 long. Anterior eye row 2.20 wide, posterior 2.00 wide. AME 0.70 in diameter. Clypeus 0.45 high. Chelicera dark brown (Fig 3) with short mastidions pointed forward; 3 posterior cheliceral teeth, 2 anterior cheliceral teeth. Palp: femur curved with dorsal bump (Fig 4); tibia with quiet short rounded RTA (Figs 5, 7, 11-12); embolus emerging from proximal tegulum with median portion slightly narrowed (Fig 6). Legs 1342 (10.00/6.90/7.80/7.50). Length of femur I 2.80, II 2.20, III 2.60, IV 2.40. Patella + tibia I 4.30, II 2.70, III 2.70, IV 2.40. Metatarsus + tarsus I 2.90, II 2.00, III 2.50, IV 2.70.

Abdomen pale with median longitudinal light stripe (Figs 1, 16) and ventrally with median longitudinal dark brown stripe. Spinnerets light brown.

Variation Male (n=3)

Total length: 6.00-7.10. Carapace length: 3.05-3.20. Length of leg I 9.05-10.00.

Female (AR 16170)

Total length: 9.00. Carapace light brown with darker cephalic area, base of the cephalothorax bearing dark spots (Fig 2), 3.90 long, 2.70 wide, 2.00 high. Ocular quadrangle 1.90 long. Anterior eye row 2.40 wide, posterior 2.10 wide. AME 0.80 in diameter. Clypeus 0.30 high. Chelicera dark brown with no mastidion; 3 posterior cheliceral teeth, 4 anterior cheliceral teeth. Legs 1-432 (8.60/8.60/8.40/6.90). Length of femur I 2.60, II 2.30, III 2.90, IV 2.90. Patella + tibia I 3.70, II 2.80, III 3.00, IV 3.00. Metatarsus + tarsus I 2.30, II 1.80, III 2.50, IV 2.80. Epigyne with a pair of oblique copulation openings, long digitiform gland ducts and long and thin copulation ducts.

Variation Female (n=6)

Total length: 6.20-9.00. Carapace length: 2.70-3.90. Length of leg I 7.30-8.60.

Distribution

Only known from French Guiana.

Comments

Type specimen and paratype were caught during mating behaviour in a building at the Nouragues field station.

DNA sequences and phylogenetic analysis.

The COI alignment was 442 base pairs (bp) long and included 92 variable sites of which 72 were informative in parsimony. The BI and ML topologies are congruent; there was no topological conflict detected between the 50% Bayesian majority-rule consensus tree (Fig. 18) and the ML bootstrap 50% majority-rule consensus tree (not shown). The topology we obtained showed (1) that the two individuals of *H. olympeae* **sp. nov.** included in the study form a strongly supported monophyletic grouping (PP = 1; BS = 100), highly divergent from the two other clades in the tree, (2) that the four accessions sampled for *H. porcatus* are part of a strongly supported clade (PP = 1; BS = 99) resolved as sister to *H. olympeae* **sp. nov.** but with poor support (PP = 0.81; BS = 67) and (3) that the 6 accessions identified as *H. taczanowskii* (3 male and 3 female individuals) were all included in a monophyletic grouping strongly supported in BI (PP = 0.99; BS = 74). The analysis of COI sequences then confirms the current morphological circumscriptions for the three *Hypaeus* species sampled here. Also, the branch lengths observed between the three clades recognized here are relatively high when compared with the magnitude of the divergence between the ingroup (*viz.* genus *Hypaeus*) and the outgroup (*viz.* *Sarinda cutleri*); this further supports the recognition of *H. olympeae* **sp. nov.** as a distinct species.

Addition to the French Guiana's jumping spiders' list

According to Vedel *et al.* (2013), Courtial *et al.* (2014) and Logunov (2015) we add nine new species for French Guiana.

Eustiromastix moraballi Mello-Leitao, 1940

RNN Nouragues, camp Pararé (4°02'N, 52°41'W), 1♂, 06.XII.2013, Canard Alain, Courtial Cyril, Leroy Boris, Pétilion Julien & Vedel Vincent, at sight in low vegetation.

Lyssomanes tenuis Peckham & Wheeler, 1889

RNN Nouragues, camp Inselberg (4°05'N, 52°41'W), 1♂, 08.XII.2013, Courtial Cyril, by beating by beating the lower branches of trees.

Scopocira abaporu Costa & Ruiz, 2014

Nouragues, Camp Pararé (4°02'N, 52°41'W), 1♂, 13.XII.2013, Courtial Cyril, by beating the lower branches of trees.

Scopocira histrio Simon, 1900

Nouragues, camp Inselberg (4°05'N, 52°41'W), 1♀, 10.XII.2013, Courtial Cyril, by beating the lower branches of trees. Nouragues, camp Pararé (4°02'N, 52°41'W), 1♂, 06.XII.2013, Canard Alain, Courtial Cyril, Leroy Boris, Pétilion Julien & Vedel Vincent, by beating the lower branches of trees.

Colonus germaini Simon, 1900

Nouragues, camp Pararé (4°02'N, 52°41'W), 1♀, 12.XII.2013, Courtial Cyril, by beating the lower branches of trees.

Corcovetella aemulatrix Galiano, 1975

Kourou, degrad saramak (5°01'N, 52°41'W), 1♀, collection date unknown, Vedel Vincent, by beating vegetation in garden near primary forest.

Pachomius nigrus Caporiacco, 1947

RNN Trinité, camp Aya (04°36'N, 53°24'W), 1♂, X.2010, Canard Alain, Courtial Cyril, Leroy Boris & Ysnel Frédéric, by beating the lower branches of trees.

Gypogyna forceps Simon, 1900

After examination of species described by Caporiacco (1954) deposited in the MNHN, the type species of *Cyllodania fasciata* (Caporicaco, 1954), considered as a subadult by Caporiacco (1954) and Galiano (1977) is in fact an adult female of *Gypogyna forceps* Simon, 1900 (Caporiacco, 1954: 150, f.48, French Guiana, Saint-Jean du Maroni, 1914, Benoist *leg*). *Cyllodania fasciata* (Caporicaco, 1954) is here presented as a new synonym of *Gypogyna forceps* Simon, 1900.

Kourou, degrad saramak (5°01'N, 52°41'W), 1♀, collection date unknown, Vedel Vincent, by beating vegetation in garden near primary forest.

Marma nigratarsis (Simon, 1900)

Saül (3°37'N, 53°12'W), 1♂, 08.X.2013, 1♂, 18.X.2013, Bellanger Yannick (Asper Society).

Acknowledgements

The authors thank Marguerite Delaval (Office National des Forêts, ONF) and ONF for funding the expedition to the Trinité National Nature Reserve; Christine Rollard and Christophe Hervé (Museum National d'Histoire Naturelle – Paris) for allowing access to the bibliography of the Arthropod laboratory and permitting the consultation of Caporiacco and Simon's collection; and Alain Canard, Boris Leroy, Frédéric Ysnel and Vincent Vedel for field support; Manuel Plantegenest, Yoann Navasse and El Aziz Djoudi (Agrocampus Ouest – Rennes) for laboratory access and technical support.

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APPENDIX.4

Non-native spiders change assemblages of Hawaiian forest fragment kipuka over space and time

Julien Pétilion, **Kaïna Privet**, George K. Roderick, Rosemary G. Gillespie & Donald K. Price
Neobiota (2020) **55**, 1-9.

Abstract

We assessed how assemblages of spiders were structured in small Hawaiian tropical forest fragments (Hawaiian, *kipuka*) within a matrix of previous lava flows, over both space (sampling kipuka of different sizes) and time (comparison with a similar study from 1998). Standardized hand-collection by night was carried out in May 2016. In total, 702 spiders were collected, representing 6 families and 25 (morpho-)species. We found that the number of individuals, but not species richness, was highly correlated with the area of sampled forest fragments, suggesting that kipuka act as separate habitat islands for these predatory arthropods. Species richness was significantly lower in the lava matrix outside the kipuka compared to the kipuka habitats, although there was no statistical difference in species composition between the two habitats, largely because of similarity of non-native species in both habitats. Over the last 20 years, the abundance of non-native spider species substantially increased in both kipuka and lava habitats, in marked contrast to the vegetation that has remained more intact. With endemism of terrestrial arthropods reaching over 95% in native forests, non-native predatory species present a critical challenge to the endemic fauna.

Key-words: Araneae; diachronic study, island.

Introduction

Kipuka are small tropical forest fragments surrounded by recent lava flows on Hawaiian islands. Many of these kipuka are rich ecosystems that have been previously investigated for their importance for native passerine birds, plants (trees and ferns) and picture-winged flies (e.g., Muir & Price 2008). Due to their spatial arrangement in a volcanic matrix, kipuka can be considered as islands within islands (Tielens et al. 2019), and thus consequently important, and original, to test classical assumptions regarding the combined effects of area and isolation on species assemblages.

The kipuka system might also be used to examine whether such particular habitats retain a strong biotic resistance to non-native species. In Hawaii, due to the remote localization of this archipelago, there are well known impacts of non-native species, with most of these studies focusing on changes in ecosystem structure (e.g., Krushelnycky & Gillespie 2008). Indeed, multiple ecological impacts of non-native flora and fauna threaten communities world-wide, and can be potentially even damaging to island systems (Vitousek 1988). Although some non-native species are reported from kipuka (e.g., rats and other mammals), kipuka appear to be less vulnerable to non-native than other (lowland) habitats, with, for example, non-native plant species almost entirely absent from kipuka (Flaspohler et al. 2010). To the best of our knowledge, no study has yet assessed how non-native spiders colonized kipuka, although they represent a major group of predators in this habitat, potentially reducing native populations.

In this study, we examined how assemblages of spiders are structured over space (e.g., comparisons across kipuka as well as lava matrix), but also potentially changed over time (in comparison to a previous study during the 1990s in the same study site: Vandergast & Gillespie 2004). We tested the general hypothesis suggested by observations of relatively intact native biota (Krushelnycky & Gillespie 2008, Flaspohler et al. 2010), that kipuka function as islands with strong biotic resistance to arthropod non-native species. More precisely, our expectations are that 1) abundance and species richness increase with increasing kipuka area, 2) species composition and richness differ between kipuka habitat and the surrounding areas and 3) despite an overall increase in non-native spider species over the last decades, the increase being less in kipuka habitats than outside.

Materials and methods

Study site and collecting

Fieldwork was conducted on the youngest and largest island of the Hawaiian Archipelago, Hawaii or the Big Island. The Kipuka system investigated consists of forest fragments surrounded by an 1855-1856 lava flow originating from Mauna Loa Volcano (19°40'01"N 155°20'56"W). These forest fragments grow on 3,000-5,000 years BP soil (Vitousek 2004), range in age from approximately 750-1,500 year BP and were most likely connected before the 1855-1856 flow that currently surrounds them (Trusdell & Lockwood 2017). These kipuka

occur within the State of Hawaii Forest Reserve System (Upper Waiakea Forest Reserve), along the Daniel K. Inouye Highway (formerly Saddle Road; mile marker 16-18, Kaumana Trail).

The forest fragments' plant species composition is relatively constant across forest fragments (Raich *et al.* 1997) and is categorized as mesic to wet *ohia* (*Metrosideros polymorpha*, Myrtaceae) forest (Jacobi & Warshauer 1990). Soil characteristics are also quite constant across fragments (Raich *et al.*, 1997) but soil nutrient conditions may vary (Vannette *et al.* 2016). Surrounding these fragments, the lava matrix is a rough textured patchwork of undulating mounds of smooth lava and free chunks of very angular pieces, extremely porous where the vegetation is sparser and poorer than those of the fragments (for a detailed description of both habitats, see Vandergast & Gillespie, 2004; Flaspohler *et al.*, 2010; Vaughn *et al.*, 2014).

Vegetation-dwelling assemblages of spiders were collected in May 2016 in the kipuka fragments and outside, in the surrounding lava, of five small (<1 ha) and five large forest patches (2-11 ha). along the Saddle Road (mile marker 16-18: Kaumana trail). The influence of kipuka area on both species richness and abundance of spiders was tested using linear regressions. Kipuka area was estimated using airborne LiDAR (Light Detection and Ranging) technology as reported by Flaspohler *et al.* (2010).

Field collection involved beating vegetation at night, the best time for collecting spiders. Each kipuka and surrounding lava was sampled by 2 people for a total of 30min, a time determined following initial sampling. Individuals were collected in separately in ethanol for identification to species or morpho-species (i.e., spider family) level at the lab. During identification, specimens were checked against voucher specimens obtained/used in the previous study (Vandergast & Gillespie, 2004). All specimens are stored at the University of Rennes, France.

Data analysis

The influence of kipuka size on both species richness and abundance of spiders was tested using linear regressions. Paired T-tests and Permanova (1000 permutations) were used to test for differences in species richness and composition, respectively, between the two habitat types. Non-metric multi-dimensional scaling ordination was used to visualize spider assemblages in the two habitats. 'Indigeneity status' was assessed using multiple bibliographic sources (see details in Vandergast & Gillespie, 2004), combined with the expertise of one of the authors (RG). Proportion of native vs non-native species were compared between kipuka and lava habitats in the same area in 2016 in 1998 (from Vandergast & Gillespie, 2004) using χ^2 tests. To allow a direct comparison of kipuka and lava habitats with previous sampling we pooled the two kipuka sampling categories of "core" and "edge" reported in the earlier study.

Results

In total, 702 spiders belonging to 6 families and 25 (morpho-) species were collected (see details in Table 1).

Tableau 1 : Number of individuals, status (Na=Native, Nn=Non-native, *: species not found in 1998, according to Vandergast & Gillespie 2004) and code of spider taxa collected inside and outside the kipuka.

Family	Genus	species	Status	Nind (kipuka)	Nind (lava)	Code
Araneidae	<i>Cyclosa</i>	<i>sp.</i>	Na	21	51	Cycsp
	<i>Neoscona</i>	<i>sp1</i>	Nn	42	1	Neosp1
	<i>Neoscona</i>	<i>sp2</i>	Nn*	23	31	Neosp2
Linyphiidae	<i>Agyneta</i>	<i>sp.</i>	Nn*	3	0	Agysp
Miturgidae	<i>Cheiracanthium</i>	<i>sp.</i>	Nn*	1	13	Chesp
Philodromidae	<i>Pagiopapulus</i>	<i>sp.</i>	Na*	4	0	Pagsp
Tetragnathidae	<i>Tetragnatha</i>	<i>acuta</i>	Na	56	85	Tetac
	<i>Tetragnatha</i>	<i>anuenue</i>	Na	43	44	Tetan
	<i>Tetragnatha</i>	<i>brevignatha</i>	Na	26	0	Tetbr
	<i>Tetragnatha</i>	<i>hawaiiensis</i>	Na	21	0	Tetha
	<i>Tetragnatha</i>	<i>quasimodo</i>	Na	27	6	Tetqu
	<i>Tetragnatha</i>	<i>spp.</i>	Na	2	0	Tetsp
Theridiidae	<i>Argyrodes</i>	<i>sp.</i>	Na	1	0	Thesp7
	<i>Ariamnes</i>	<i>spp.</i>	Na*	59	1	Argsp
	<i>Steatoda</i>	<i>grossa</i>	Nn*	11	0	Stegr
	<i>Theridion</i>	<i>grallator</i>	Na	20	0	Thegr
	<i>Theridion</i>	<i>sp1</i>	Na	23	35	Thesp1
	<i>Theridion</i>	<i>sp2</i>	Na	8	2	Thesp2
	<i>Theridion</i>	<i>sp3</i>	Na	1	0	Thesp3
	<i>Theridion</i>	<i>sp4</i>	Na	4	2	Thesp4
	<i>Theridion</i>	<i>sp5</i>	Na	4	6	Thesp5
	<i>Theridion</i>	<i>sp6</i>	Na	2	3	Thesp6
Thomisidae	<i>Mecaphesa</i>	<i>sp1</i>	Na*	1	3	Mecsp1
	<i>Mecaphesa</i>	<i>sp2</i>	Na*	4	10	Mecsp2
	<i>Synaema</i>	<i>sp.</i>	Na*	1	1	Synsp

Kipuka size had a large effect on the number of individuals (linear regression, $Y = 5.58X(\text{ha}) + 27.4$, $R^2 = 0.93$, $p < 0.001$, 9df), but no effect on species richness (linear regression, $R^2 = 0.12$, NS, 9df). Species richness of spiders was significantly higher in kipuka habitats compared to the surrounding lava (mean \pm se: 10.8 ± 0.6 vs. 6.8 ± 0.6 respectively; Paired T-test, $t = 6.34$, 9 df, $p < 0.001$), although there was no statistical difference in species composition between the two habitat types (Permanova: $F_{1,8} = 0.06$, $p = 0.349$, Fig. 1). The proportion of non-native spider species increased significantly between 1998 and 2016, in both kipuka and lava habitats (χ^2 tests, $\chi^2 = 67.53$, 1 df, $p < 0.001$ and $\chi^2 = 4.34$, 1 df, $p < 0.037$ respectively), with a higher increase in kipuka habitats (see Fig. 2). This increase in both habitat types was due to both an increase in the number of non-native species and a particular increase in the number of individuals of few species (e.g., *Steatoda grossa*: Table 1).

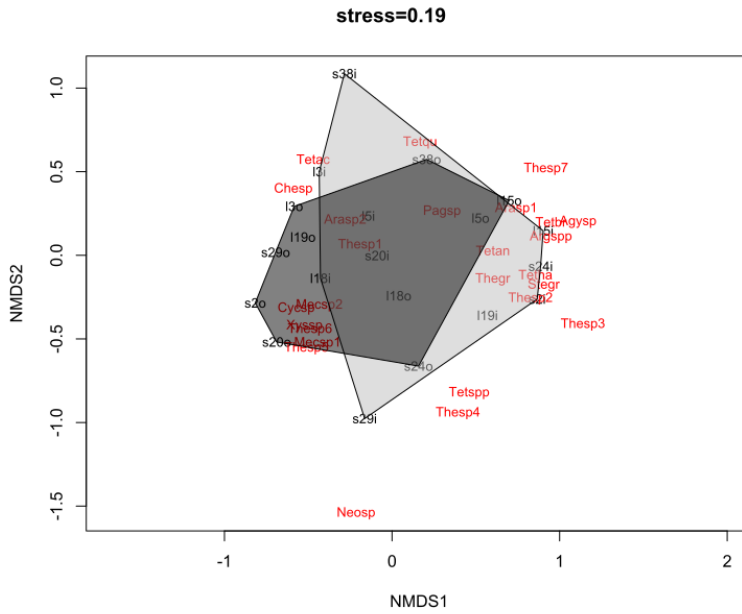


Figure 1 : Non-metric multi-dimensional scaling ordination of spider assemblages from kipuka habitats (grey ellipsoid) and surrounding lava (black ellipsoid). Species are in red and sampling stations in black. Stress=0.189.

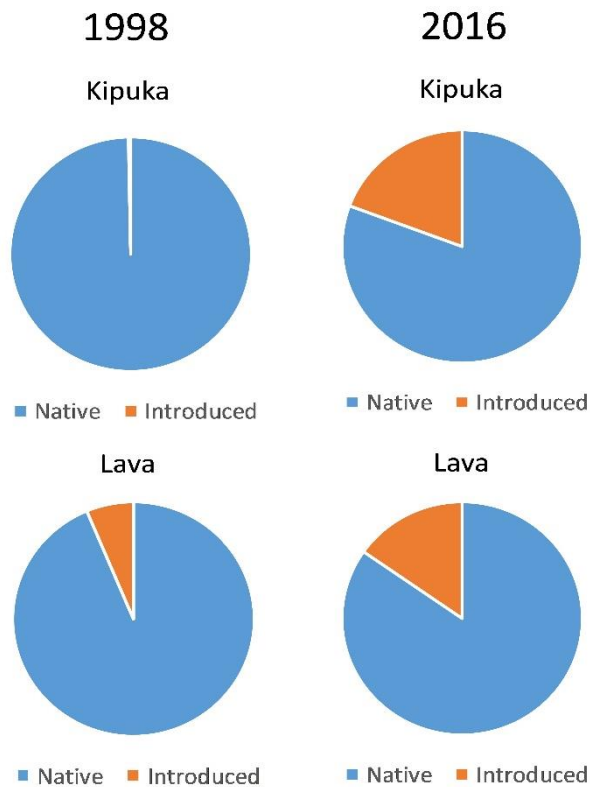


Figure 10 : Relative abundance of native (blue) and non-native (orange) species in kipuka habitats and surrounding lava, in 1998 (430 individuals) and in 2016 (702 individuals). For spider taxa code, see Table 1.

Discussion

The total number of individuals across all spider species was strongly associated with the area of sampled forests, suggesting that kipuka act, at least partly, as separate habitat islands for the spiders. Yet, as recently observed for entire arthropod communities in the same area (Tielens et al. 2019), spider species richness was not a function of kipuka size. Indeed, spider species in kipuka habitats tend to be found in all such habitats (Vandergast & Gillespie 2004, Vandergast et al, 2004). These two results altogether suggest that kipuka act as islands for native species in a hostile matrix. Yet, the abundance of several native and non-native species was found to be high in both kipuka habitats and surrounding lava, leading to overlapping, and statistically indistinguishable, assemblage compositions (see also Tielens et al. 2019). Fragment size is known to be a strong determinant of the structure of the forest in the kipuka (Vaughn et al., 2014) with larger fragments having greater average height, larger diversity of height and lower edge to core habitat being thus less affected by the matrix overall. Kipuka edges are also known to house different species from the kipuka interiors (Vandergast & Gillespie 2004). For example, more native *Drosophila* are found in large kipuka while more non-native *Drosophila* and other insects are found in small kipuka (Mueller 2015). Patch size, on top of influencing habitat quality, is also known to act on migration rates, and the linear relationships between kipuka area and number of spider individuals can be also be the result of immigration-emigration dynamics (Hambäck & Englund 2005).

There was an important increase in the proportion of non-native species over time, while no native species disappeared between the two sampling periods. Several new species like *Cheiracanthium* sp. and *Steatoda grossa* were detected in this study, i.e. they were not recorded in the same study site twenty years ago. Other species have an unclear biogeographic and taxonomic status, e.g., *Agyneta* sp., which shows that more intensive studies are still needed on the Hawaiian archipelago (Gertsch 1973). The kipuka we sampled belong to the State of Hawaii Forest Reserve System (Upper Waiakea forest reserve), an area subject to limited anthropogenic disturbance for the last 160 years, but importantly located along the Daniel K. Inouye Highway that was reconstructed in 2008 and 2011. Thus, the increase of non-native species is likely associated with previous construction activity and more road traffic along the renovated highway. Non-native arthropods in Hawaii respond more quickly to disturbance than their endemic counterparts (Gillespie et al, 2008) and are known to follow pathways of human activity (Krushelnycky & Gillespie 2008). Interestingly, the increase in non-native spiders was actually higher in kipuka habitats compared to the outside lava, rejecting our hypothesis of a stronger biotic resistance to non-native species in intact forest fragments, and in marked contrast to the relatively intact flora of these habitats. Kipuka offer many micro-habitats for new comers, for example, bark of *Metrosideros polymorpha* where *Steatoda grossa* are often found in numbers, as well as complex edge habitats where one species of non-native spiders was found previously (Vandergast & Gillespie 2004).

In conclusion, kipuka function as habitat islands within islands, with many island-like features such as a characteristic biota, unique microclimate, and biological associations with

increasing area. Kipuka, likely other islands also appear to be vulnerable to non-native species, especially compared to surrounding lava habitats. Until now native species of spiders do not seem affected by these new comers, but spiders can have a large impact on prey species because they are ecologically dominant and generalist predators in a large variety of habitats (Pekár & Toft 2015), including tropical forests (Coddington et al. 2009). In Hawaii, with a large number of endemic species (Howarth 1990, Eldredge and Evenhuis 2003), non-native spiders are a critical challenge for management. The impact of these new generalist predators on the structure and functioning of kipuka is currently investigated using meta-barcoding and NGS techniques. We are also planning to look at other spider associates, including parasite occurrence in spiders (see Vandergast & Roderick 2003), to see how the associated community has changed together with increased non-native species.

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My research focusses on ecological and evolutionary patterns of spider diversity and the processes at their origin, in tropical forests and more recently on the Hawaiian archipelago.

EDUCATION

- Ph.D** Ecology & Evolution, University of Rennes, France, with Honors, 2017-2021
- M.S** Functional, Behavioral and Evolutionary Ecology, Modeling in Ecology, Natural Heritage and Biodiversity, University of Rennes, France, with Honors, 1st/19 students, 2013-2017
- B.S** Organisms Biology, University of Rennes, France, with Honors, 2011-2013

TEACHING EXPERIENCE

- 2017-2018** Teaching Assistant – (64 hours) University of Rennes.
- Ecology, communities and ecosystems functioning, statistic tools and spatial analysis applied to ecology

RESEARCH EXPERIENCE

- Since 2017** Multiscale factors structuring diversity in taxa, traits and evolutionary units of spiders in tropical environments – PhD (4 years), team Landscape and Climate Change, Ecobio, UMR CNRS - University of Rennes
with J. Pétilion & R. Gillespie
- 2017** Evolutionary and functional dynamics of the lupines (Fabaceae) LysM receptor gene in a context of change of specificity in the nitrogen fixing symbiosis – MSc internship (6 months), team Evolution, Genomes and Adaptation, Ecobio, UMR CNRS - University of Rennes.
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- 2016** Molecular phylogeny of undetermined Orchids of the genus *Ophrys* – Voluntary internship (4 months), team Evolution, Genomes, Adaptation, Ecobio, UMR CNRS - University of Rennes.
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- Modeling landscape connectivity from different algorithms – MSc internship (3 months), team Landscape and Climate Change, Ecobio, UMR CNRS - University of Rennes.
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- 2015** How diverse is tropical biodiversity? Standardised comparison of tropical and temperate spider assemblages and insight of molecular approach in species richness study – MSc internship (6 months), team Biodiversity and landscape management, EA 7316, University of Rennes.
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- 2014** Ecological and methodological analysis of spider assemblages of Les Nouragues Nature Reserve, French Guiana – MSc internship (3 months), team Biodiversity and landscape management,, EA 7316 University of Rennes.
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PEER-REVIEWED PUBLICATIONS

1. Keller J. Imperial J., Ruiz T., **Privet K.**, Lima O., Salmon A., Ainouche A. and F. Cabello-Hurtado (2018). Sequencing and analysis of three *Lupinus* nodulome provides new insight on the specific relationships with compatible and non-compatible *Bradyrhizobium*. *Plant Science*, **266**, 102-116.
2. **Privet K.**, Courtial C., Decaëns T., Djoudi E.A., Vedel V., Ysnel F. and J. Pétillon (2018). Spider community structure in a neotropical rainforest-inselberg complex : ecological and methodological insights from a small-scale intensive survey. *Journal of Tropical Ecology*, **59**, 21-34.
3. **Privet K.**, Vedel V., Fortunel C., Cerdan A., Martinez Q., Barraloto C., Petitclerc F., Orivel F. & J. Pétillon (2020). Relative efficiency of pitfall trapping vs. hand-collecting along a structural gradient of neotropical habitats. *Diversity*, **12**, 81 (special issue “Systematics and Evolution of Spiders”).
4. Pétillon J., **Privet K.**, Vandergast A., Gillespie R. and D. K. Price (2020). Changes in spider assemblages of Hawaiian forest fragments over space and time. *Neobiota*, **55**, 1-9.
5. **Privet K.**, and J. Pétillon (2020). First quantification of the difference in spider diversity between tropical vs. temperate forests. *Ecology and Evolution*, **10**, 13165– 13172.
6. Lowe E., Wolff J., ... **Privet K.**, ... and M. Herberstein (2020). Towards establishment of a centralized spider traits database. *Journal of Arachnology*, **2**, 103-109.
7. Pekár S., Wolff J., ..., **Privet K.**, ..., E. Lowe. The World Spider Trait Database (WST): a centralised global open repository for curated data on spider traits. *Database*, **2021**, baab064.
8. Courtial C., **Privet K.**, Picard L. and J. Pétillon. Description of new species of *Hypaeus* Simon (Araneae, Salticidae, Amycinae) based on integrative taxonomy. Submitted to *Studies on Neotropical Fauna and Environment*.
9. **Privet K.**, Hamrik T., Lamarre G, and J. Pétillon. Complementary of taxon- and trait-based metrics to understand tropical diversity – A case study using spider assemblages of Neotropical forests habitats. *In prep.*
10. **Privet K.**, Pétillon J., Rosemary G., and H. Krehenwinkel. Phylogenetic relationships among Hawaiian wolf spiders suggest recent radiation influenced by the adaptation to different environments. *In prep.*
11. Lalagüe H., Fortunel C., **Privet K.**, Védél V. and J. Pétillon. Unexpectedly high contribution of vertical vs. horizontal strata to spider diversity in Amazonian forests. *In prep.*

COMMUNICATIONS

1. **Privet K.**, and J. Pétillon (2018). Differences in tropical vs. temperate diversity in arthropod predators provide insights into causes of latitudinal gradients of species diversity. *International Conference on Ecological Sciences*, October 22-25 2018, Rennes (France).
2. Pétillon J., **Privet K.**, Vandergast A., Gillespie R. and D. Price (2018). Drivers of spider assemblages in Hawaiian forest fragments (Kipuka). *International Conference on Ecological Sciences*, October 22-25 2018, Rennes (France).
3. **Privet K.** & J. Pétillon (2019). Comparative patterns of taxonomic-, phylogenetic- vs. functional-based diversity metrics at small and large spatial scales. *Spider traits workshop*, February 10 2019, Christchurch (New-Zelände).
4. **Privet K.**, Krehenwinkel H., Gillespie R. and J. Pétillon (2019). Phylogeny of the wolf spiders from the island of Hawai'i inferred from multilocus genetic data. *21st International Congress of Arachnology*, February 11-15 2019, Christchurch (New-Zelände).
5. Pétillon J., **Privet K.**, Fortunel C., Cerdan A., Martinez Q., Barraloto C., Petitclerc F., Orivel F. & V. Vedel (2019). Relative efficiency of pitfall trapping vs. hand-collecting along a structural gradient of neotropical habitats. *21st International Congress of Arachnology*, February 11-15 2019, Christchurch (New-Zelände).
6. **Privet K.**, Pétillon J., Gillespie R. and H. Krehenwinkel (2021). Phylogeny of wolf spiders from the Hawaiian archipelago inferred from multilocus genetic data. *32rd European Congress of Arachnology*, August 23-26 2021, online.

GRANTS & AWARDS

International Society of Arachnology Student Travel Grant 2019 – Travel grant to assist and present at the 21st International Congress of Arachnology, 2019 in New Zealand (Christchurch).

American Arachnological Society Student Research Grant 2020 – Travel grant to do field work in Hawaii, USA in 2021.

Rennes' Doctoral School Mobility Grant 2021 (Cancelled due to Covid-19 restrictions)– Travel grant to visit Dr. Megan Porter at the Department of Biology the University of Hawai'i at Manoa.

SUPERVISION

- Marti S.L., 2020. Development of molecular analysis methods on museum spider specimens** – Assistant engineer (5 months), Ecobio, UMR CNRS / University of Rennes
- Berlier L., 2019. Functional and phylogenetic diversity of spiders in tropical forests of French Guiana** – 3rd year Bachelor student (4 months), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétilion
- Poirier A., 2019. Functional diversity of spiders from the main tropical forest habitats of the Amazon basin** – 1st year Master student (3 months), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétilion
- Salomon L., 2019. Functional diversity of spiders from the main tropical forest habitats of the Amazon basin** – 2nd year Bachelor student (1 month), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétilion
- Le Naviel A., 2018. Small and large-scale variation in spider diversity of major tropical forest habitats in French Guiana** – 1st year Master student (3 months), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétilion
- Hacala A., 2016 Specific and functional diversity of spiders across tropical forest gradient in French Guiana** – 1st year Master student (3 months), Team Biodiversity and Landscape management, EA University Rennes. Co-supervisors: C. Courtial et G. Lamarre.

Synergistic ACTIVITIES ctivities

- **PhD representative in the Lab Advisory council** – 2017-2019
- **Member of the Training committee of the Doctoral school EGAAL**–2018-2019
- **Main organizer of the symposium “Island Arachnids Biogeography”** – 21st International Congress of Arachnology, Christchurch, February 2019, co-organizers: Julien Pétilion, Rosemary Gillespie and Sarah Boyer.
- **Member of the International Society of Arachnology, the American Arachnological Society and the European Society of Arachnology** – since 2017
- **Member of the Australasian Arachnological Society and the Society for the study of Evolution** – since 2019

THÈSE DE DOCTORAT DE

L'UNIVERSITE DE RENNES 1

ECOLE DOCTORALE N° 600

Ecole doctorale Ecologie, Géosciences, Agronomie et Alimentation

Spécialité : *Écologie et Évolution*

Par

Kaïna PRIVET

« Facteurs multi-échelles structurant les diversités en taxons, traits et unités évolutives des araignées en milieux tropicaux »

Thèse présentée et soutenue à Rennes, le 3 décembre 2021

Unité de recherche : ECOBIO UMR 6553 CNRS – Université de Rennes 1

Thèse N° :

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Sandrine PAVOINE	Maître de conférence, Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, Paris, France

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TABLE DES MATIÈRES

Glossaire	1
Introduction.....	5
Étude des patterns de diversité et des processus à leur origine	5
Diversité ou diversités ?	5
Patterns et processus de diversité	3
Les trois principales composantes de la diversité.....	6
Les araignées comme modèle pour l'étude de la diversité	12
Le succès évolutif et écologique des araignées	12
Taxonomie des araignées.....	14
État de l'approche basée sur les traits chez les araignées.....	14
Phylogénie des araignées.....	19
Patterns de diversité et processus connus chez les araignées	20
Étude de la diversité des araignées en milieux tropicaux.....	22
Milieux tropicaux : hauts lieux de diversité	22
Les difficultés de l'étude de la diversité des araignées tropicales.....	22
Objectifs et organisation de la thèse	25
Partie I : Facteurs structurant la diversité taxonomique des araignées tropicales	27
CHAPITRE.1 Efficacité relative des pièges barbers par rapport à la chasse à vue de nuit dans l'évaluation de la diversité des araignées du sol le long d'un gradient structural d'habitat néotropical	29
Abstract	29
Introduction.....	30
Materials and methods	31
Results	33
Discussion.....	36
Acknowledgments.....	38
Funding.....	39
References.....	39
Supplementary Materials.....	42
CHAPITRE.2 Structure des assemblages d'araignées dans un complexe forêt humide-inselberg néotropical : aperçu écologique et méthodologique d'une étude intensive à petite échelle	45
Abstract	45
Introduction.....	46
Materials and methods	48

Results	51
Discussion	55
Acknowledgements	60
References	60
Supporting Information	65
Part II : Complémentarité des approches traits et taxons pour la compréhension des patterns de diversité des araignées tropicales	71
CHAPITRE.3 Comparaison des patterns de diversité taxonomique et fonctionnelle des araignées entre forêts tropicales et tempérées	73
Abstract	73
Introduction.....	74
Methods	75
Results	77
Discussion	79
Acknowledgements	81
References.....	82
Supporting information.....	86
CHAPITRE.4 Complémentarité des métriques basées sur les traits et sur les taxons pour comprendre les patterns de diversité tropicale – Un cas d'étude utilisant des assemblages d'araignées dans des habitats néotropicaux contrastés.....	91
Abstract	91
Introduction.....	92
Material and methods.....	94
Results	98
Discussion	106
Acknowledgements	108
References.....	109
Supplementary Materials.....	119
Part III : Décrire et comprendre la diversité des araignées tropicales par l'approche phylogénétique : le cas des araignées loups d'Hawaï.....	121
CHAPITRE.5 Les relations phylogénétiques entre les araignées-loups hawaïennes suggèrent une radiation récente due à l'adaptation à différents environnements.	123
Abstract	123
Introduction.....	124
Materials and methods	130
Results	138
Discussion	146

Acknowledgements	152
References.....	152
Supplementary materials	161
Discussion générale et perspectives	181
Discussion générale: l’habitat joue un role dans la diversité des araignées tropicales.....	181
Perspectives de recherche	184
Recherches supplémentaires sur les règles d’assemblage des araignées tropicales	184
Repenser l’échantillonnage en milieu tropical : la nécessité d’utiliser un ensemble de méthodes d’échantillonnage dans des protocoles standardisés.....	186
Importance de la taxonomie	187
Vers le développement d'une approche basée sur les traits adaptée aux écosystèmes tropicaux.....	188
Utilisation du NGS pour résoudre des relations évolutives complexes.....	188
Conclusion	189
References.....	191
Articles annexes	209
ANNEXE.1 Vers l’établissement d’une base de données centralisée sur les traits des araignées	209
Abstract	209
Introduction.....	210
General database benefits	211
Benefits of a spider traits database	212
Logistics of a traits database	213
Additional challenges for a spider traits database.....	216
Potential research that would become feasible with a spider traits database	216
Outlook.....	217
Acknowledgements	218
Litterature cited.....	218
ANNEXE.2 La base de données World Spider Trait (WST) : un référentiel mondial ouvert et centralisé pour les données sur les traits des araignées	223
Abstract	223
Background & Summary.....	224
Methods	225
Data Records	229
Technical Validation	232
Usage Notes	233

Code Availability	234
Acknowledgements	234
References	234
Supplementary information	237
ANNEXE.3 Nouvelle espèce de <i>Hypaeus</i> Simon (Araneae : Salticidae : Salticinae : Amycini) basée sur la taxonomie intégrative	249
Abstract	249
Introduction.....	250
Material and Method	251
Results	254
Acknowledgements	261
References.....	261
ANNEXE.4 Les araignées exogènes modifient les assemblages trouvés dans les kipuka, fragments de forêts Hawaïien, dans l'espace et le temps	265
Abstract	265
Introduction.....	266
Materials and methods	266
Results	267
Discussion	270
Acknowledgments	271
References.....	271
Curriculum Vitae.....	273

GLOSSAIRE

Assemblage : groupe taxonomiquement apparenté de populations d'espèces qui sont trouvées ensemble dans l'espace.

Biogéographie : étude des schémas/patterns de distribution de diversité des organismes et des écosystèmes dans l'espace et le temps, ainsi que des facteurs qui déterminent ces schéma/patterns. C'est un champ d'étude à la croisée de la systématique, de l'écologie, de l'évolution et de la phylogéographie.

Communauté : groupes d'organismes qui vivent ensemble dans l'espace et le temps et qui interagissent entre eux.

Diversité : variété des êtres vivants en termes d'unités taxonomiques, de traits et d'unités évolutives, à des échelles d'espace et de temps.

Écologie des communautés : étude des patterns de diversité, abondance et composition des espèces dans les communautés ainsi que des processus à l'origine de ces patterns et du fonctionnement des communautés (e.g. interactions biotiques).

Espèces : lignées de populations ou métapopulations qui évoluent séparément.

Facteurs : chacun des paramètres ou composantes de l'environnement qui affectent les organismes et le fonctionnement de l'écosystème et donc la répartition, l'abondance et l'évolution de la biocénose. Ils peuvent être biotiques (e.g. relations trophiques, compétition) ou abiotiques (e.g. composantes chimiques et physiques de l'environnement comme le climat, la topographie). Les facteurs influencent les processus qui déterminent les patterns de diversité.

Filtrage d'habitat : exclusion des espèces dont les combinaisons de traits sont inappropriées pour des conditions abiotiques et biotiques données.

Hyperdiversifié (ou megadiversifié) : « qui présente une grande diversité ». Terme s'utilisant pour une unité du vivant (groupe, taxon, assemblage, communauté) ou une zone (habitat, environnement, milieu, pays) et qui réfère à la quantité d'unité (souvent espèces). Utilisé pour la 1ère fois lors d'une conférence sur la biodiversité (Smithsonian Institution, Washington) pour décrire des pays qui présentent au moins 5 000 espèces endémiques.

Morpho-espèces : groupements d'individus similaires, catégorisés sur la base de caractéristiques de la morphologie externe, sans recours à la taxonomie.

Niche : ensemble de conditions environnementales, i.e. physiques (e.g. habitat, température, humidité, pH) et de ressources (e.g. type particulier de nourriture, taille de nourriture), des lequel des populations stables peuvent se maintenir.

Para-taxonomie : approche qui consiste à grouper des organismes à « l'espèce » sur la base de caractéristiques de morphologie externe, sans considérer la taxonomie. Ces groupes sont appelés des morpho-espèces. Cette approche est utilisée dans les cas où la littérature et/ou les spécialistes du groupe d'intérêt ne sont pas consultés, disponibles ou existants.

Patterns de diversité : arrangement des composantes de la diversité (i.e. taxon, traits et unités évolutives) à une échelle du vivant, e.g. variation de la diversité taxonomique entre communautés. On distingue deux types de pattern : spatial et temporel. Ces patterns sont le résultat de processus écologiques et évolutifs.

Processus (à l'origine des patterns de diversité) : processus

- Dont l'intensité varie en fonction des changements de l'environnement
- Qui influencent différemment des processus secondaires (e.g. taux de spéciation, degré de spécialisation, étendue ou recouvrement de la niche, structure de la communauté) dans différents environnements

Ces processus sont supposés contrôler directement ou indirectement les patterns de diversité observés. On distingue les processus à l'origine de la diversité, qui sont les processus qui influencent la diversification, et ceux à l'origine des patterns de la diversité, qui influence sa structuration dans l'espace et le temps. On peut aussi catégoriser les processus selon qu'ils sont déterministes ou stochastiques, écologiques ou évolutifs.

Processus déterministes : tout processus qui fait intervenir des mécanismes non aléatoires, fondés sur la niche. E.g. : filtre d'habitat, compétition, prédation.

Processus stochastiques : tout processus qui donne lieu à des patterns de diversité, d'abondance et de composition en espèces qu'il est impossible de distinguer du seul hasard. E.g. : dérive génétique ou écologique, dispersion.

Processus écologiques : les interactions entre les individus d'une même espèce ou d'espèces différentes et entre eux et leur environnement, qui déterminent la dynamique des populations, des communautés et des écosystèmes sur une échelle de temps écologique, généralement sur quelques générations. E.g. : processus climatiques, productivité, effet de l'habitat sur la diversité, interactions entre organismes.

Processus évolutifs : tout processus conduisant à des changements génétiques dans les populations, entraînant la divergence et la persistance des lignées sur une échelle de temps évolutive, s'étendant généralement à de nombreuses générations. E.g. : sélection (sexuelle et naturelle), dérive génétique, mutations, flux de gènes.

Taxonomie intégrative : la science qui vise à délimiter les unités de la diversité du vivant (e.g. espèces, genres, familles) à partir de perspectives multiples et

complémentaires comme la phylogéographie, la morphologie comparée, la génétique des populations, l'écologie, le développement, les comportements.

Traits : caractéristiques morphologiques, anatomiques, biochimiques, physiologiques ou phénologiques mesurables au niveau individuel qui reflètent le résultat de processus d'évolution et d'assemblage de communautés répondant à des contraintes environnementales abiotiques et biotiques.

INTRODUCTION

Étude des patterns de diversité et des processus à leur origine

Comprendre l'origine des patterns de diversité biologique est l'un des défis majeurs de l'écologie moderne. Des champs entiers de l'écologie y sont dédiés, que ce soit pour comprendre les patterns de diversité¹ des organismes et les processus² qui en sont responsables à l'échelle des communautés (écologie des communautés) ou à des échelles plus larges de temps et d'espace (phylogéographie, biogéographie). Dans cette première partie nous nous concentrons à donner une définition du concept de diversité, à présenter l'état des connaissances sur les patterns et processus de celle-ci, ainsi qu'à décrire les principales composantes de la diversité.

Diversité ou diversités ?

Définition

La diversité est un concept riche, qui comprend un grand nombre de définitions possibles (Harper & Hawksworth 1994, DeLong 1996). Dans sa forme la plus large, la diversité (voir **encadré 1** pour la différence avec biodiversité) peut être vue comme la variation ou l'hétérogénéité des êtres vivants, à toutes les échelles et à tous les niveaux d'organisation : des variations entre individus jusqu'à l'infinie complexité constituée par l'assemblage d'innombrables communautés qui peuplent la biosphère (Faith 2016). Cela inclut par exemple les diversités spécifique, fonctionnelle, génétique et phylogénétique. Il existe donc de très nombreuses composantes de la diversité et il est impossible de décrire « la » diversité comme un simple ordre de grandeur (Gaston & Spicer 2013). Pourtant, le mot diversité a été très souvent utilisé comme synonyme de diversité en espèces, et les autres composantes ont été moins explorées en écologie (Colwell 2009, Pavoine & Bonsall 2011). Les progrès faits ces dernières années, e.g. en terme de production de phylogénie moléculaires ou d'étude des traits, ont largement amélioré notre compréhension de l'importance de la prise en compte des relations phylogénétiques et des traits fonctionnels dans la diversité (e.g. Violle *et al.* 2007, Cavender-Bares *et al.* 2009, Mouquet *et al.* 2012). La diversité a alors été redéfinie comme « un concept complexe à multiples facettes qui comprend des échelles d'espace et de temps, et

¹ Arrangement des composantes de la diversité (i.e. taxon, traits et unités évolutives) à une échelle du vivant, e.g. variation de la diversité taxonomique entre communautés. On distingue deux types de pattern : spatial et temporel. Ces patterns sont le résultat de processus écologiques et évolutifs.

² Processus dont : (1) l'intensité varie en fonction des changements de l'environnement, (2) influencent différemment des processus secondaires (e.g. taux de spéciation, degré de spécialisation, étendue ou recouvrement de la niche, structure de la communauté) dans différents environnements. Ces processus sont supposés contrôler directement ou indirectement les patterns de diversité observés (Osman & Whitlatch 1978).

des entités telles que les espèces, les traits et les unités évolutives » (Pavoine & Bonsall 2011). Nous détaillerons ces composantes (espèces, traits et unités évolutives) plus loin (voir section **Les trois principales composantes de la diversité, page 6 et suivantes**).

Encadré 1. Différence entre diversité et biodiversité

La biodiversité est un néologisme apparu lors du Forum de Washington en 1986 (mais voir par exemple un utilisation antérieure dans Faith 1970) et internationalisé en 1992 lors du Sommet de la Terre à Rio. Le concept de biodiversité est une construction scientifique, sociale et politique et a mis en évidence la nécessité de collaborer face à la crise environnementale (Charvolin & Ollivier 2017). Ce concept ne comprend donc pas uniquement la diversité du vivant, il comprend aussi la valeur de cette diversité et les interactions des êtres humains avec le vivant (Toepfer 2019). Il relie donc de nombreuses disciplines telles que la biologie, la bioéthique, la philosophie, l'économie, le droit et la politique. Ces différentes disciplines étudient en réalité différentes choses (Meinard *et al.* 2019). On étudie par exemple la diversité spécifique, fonctionnelle ou phylogénétique en écologie ; la naturalité ou la diversité perçue en économie de l'environnement et en sociologie. Aussi, Toepfer (2019) propose de considérer « biodiversité » comme une métaphore absolue comme « vie », « temps » ou « monde », expliquant ainsi que ce terme n'a pas de définition fixe car il sert de médiateur entre divers contextes et disciplines. Cette thèse se plaçant dans un cadre d'écologie scientifique, nous préférons utiliser le terme « diversité », car nous n'aborderons pas les autres facettes de la biodiversité et ne souhaitons pas que ce travail soit considéré comme une approche scientifique de la « biodiversité » (voir Sarkar 2019 pour une définition de l'approche scientifique de la biodiversité).

Les échelles de la diversité

Il existe de nombreuses **échelles d'organisation du vivant** auxquelles la diversité peut être étudiée, e.g. individu, population, communauté, méta-communauté. Parmi celles-ci, l'échelle des communautés est l'une des plus retenues dans les études sur la diversité. Les communautés sont définies comme des groupes d'organismes qui vivent ensemble dans l'espace et le temps et qui interagissent entre eux (Whittaker 1975). Dans cette thèse, on préférera l'utilisation du terme assemblages, défini comme des groupes d'organismes taxonomiquement apparentés de population d'espèces qui sont trouvées ensemble dans l'espace et le temps, sans notion d'interactions biotiques entre elles (car nous ne les avons pas étudiées), bien qu'elles puissent exister (Fauth *et al.* 1996, Magurran 2004, Stroud *et al.* 2015).

La diversité est aussi partitionnée à **des échelles spatiales** (Whittaker 1960) (**Figure 1**). Les diversités taxonomique, en traits et phylogénétique peuvent être étudiées (1) à l'échelle locale d'un assemblage ou d'un habitat, appelée diversité alpha (α), (2) entre assemblages locaux ou habitats, appelée diversité bêta (β) (voir aussi la diversité zeta (ζ), qui inclut les différentes métriques de diversité entre habitats, Hui & McGeoch, 2014), (3) à l'échelle régionale ou des méta-communautés (ensemble de communautés locales liées par la dispersion), appelée diversité gamma (γ). Ces composants ont été réutilisés par la suite pour mettre en évidence l'importance de la partition temporelle (entre années, décennies et siècles) de la diversité (Pavoine *et al.* 2009, Pavoine & Bonsall 2011, Mushet *et al.* 2019).

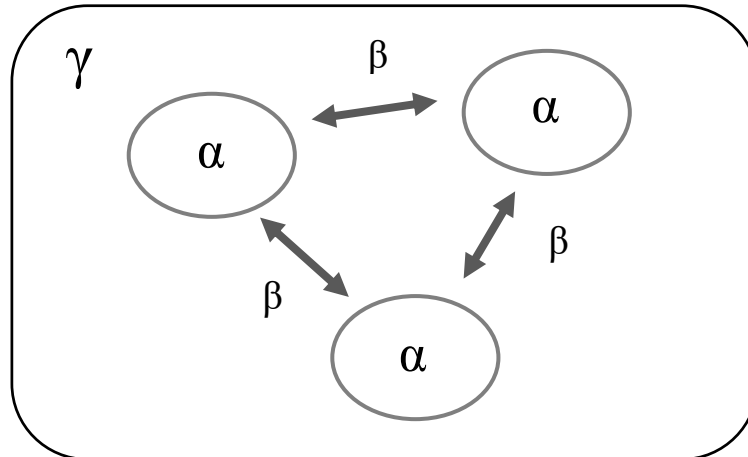


Figure 1: Partition spatiale de la diversité. La diversité gamma (γ) est la diversité de l'ensemble des assemblages à l'échelle régionale, la diversité alpha (α) la diversité d'un assemblage à l'échelle locale et la diversité beta (β) la diversité entre les assemblages. Issu de Daly et al. 2018.

Patterns et processus de diversité

Les patterns de diversité sont des arrangements spatiaux ou temporels des composantes de la diversité (i.e. espèces, traits et unités évolutives) à une échelle du vivant, e.g. : variation de la diversité en espèces entre assemblages (Scheiner 1992). Les processus à l'origine des patterns de diversité des communautés sont des processus comme la compétition, la prédation ou le filtrage d'habitat, dont l'intensité varie en fonction de l'environnement et déterminent directement ou indirectement les patterns de diversité observés (Osman & Whitlatch 1978). Il nous faut bien décrire et comprendre les patterns de diversité pour pouvoir faire des inférences sur les processus qui en sont à l'origine.

Principaux patterns de diversité

Les patterns de diversité ont été le mieux décrits pour la diversité en espèces. Cette composante de la diversité du vivant est répartie de manière hétérogène entre les taxons et à la surface de la planète.

Aux alentours de 1.43 millions d'espèces d'eucaryotes ont été décrites au sein des 10.95 millions d'espèces estimées (Mora *et al.* 2011). Environ 1% de ces espèces sont des vertébrés, 10% des plantes et 90% des invertébrés (May 2010), la moitié des invertébrés étant des arthropodes (Chapman 2009).

A la surface de la planète, la diversité varie en fonction de facteurs spatiaux tels que la latitude, la surface, l'éloignement ou de facteurs écologiques et environnementaux tels que la productivité biologique, l'altitude, l'hétérogénéité de l'habitat, la complexité de l'habitat ou les perturbations (Ricklefs & Schluter 1993). Les patterns de diversité spécifique ont été largement synthétisés (Pianka 1966, Ricklefs & Miller 1999, Willig *et al.* 2003, Vellend 2010),

et nous ne ferons ici qu'en mentionner certains pour lesquels des connaissances existent aussi pour les traits et les unités évolutives (mesurées par la diversité phylogénétique).

À une large échelle on observe, chez la plupart des organismes, une augmentation latitudinale de la diversité en espèces atteignant son maximum dans les tropiques (Willig *et al.* 2003). On sait par exemple que les forêts tropicales pourraient abriter dix fois plus d'espèces d'arbres que des forêts de biomasse similaire en région tempérée (Latham & Ricklefs 1993) et entre 2.1 et 8.4 fois plus d'arthropodes terrestres (Basset *et al.* 2012) (**Encadré 2**). Ce pattern est aussi retrouvé lorsque l'on considère la diversité phylogénétique, e.g. Fritz & Rahbek (2012), Smith *et al.* (2017), Massante *et al.* (2019) chez les amphibiens, les oiseaux et les plantes, respectivement. À l'inverse, la diversité en trait ne suit pas toujours ce gradient latitudinal. Par exemple, Schumm *et al.* (2019) ont mis en évidence que les faunes tropicales en bivalves marins et en oiseaux terrestres sont plus riches en traits mais moins régulières que celles des régions tempérées. Cardoso *et al.* (2011b) ont eux montré que la richesse en traits chez les araignées n'est pas toujours supérieure dans les régions tropicales par rapport aux régions tempérées et Lamanna *et al.* (2014) que la diversité en traits des arbres est plus élevée en milieux tempérés.

À une échelle plus locale, la diversité varie le long de gradients environnementaux comme entre habitats en fonction de leur productivité, de leur structure (hétérogénéité, complexité), de leur isolement, altitude ou de leurs conditions physiques (Ricklefs & Miller 1999). Par exemple, la diversité en espèces des araignées est plus élevée lorsque la structure de la végétation est plus hétérogène (en terme de hauteur de tiges) (Greenstone 1984). La diversité spécifique en plante est fortement liée au pH du sol (Pärtel 2002).

Il n'y a pas, à ce jour, de synthèse concernant les patterns de diversité en espèces, traits et unités évolutives. Les observations empiriques suggèrent toutefois que les diversités s'échelonnent différemment selon que l'on considère les espèces, les traits ou les unités évolutives. Les tentatives de généraliser des patterns de diversité à toutes les lignées du vivant (e.g. le gradient latitudinal de diversité Willig *et al.* 2003) ont mis en évidence que les patterns diffèrent entre groupes. Les études des patterns locaux mettent elles en évidence que les patterns varient entre régions (Pärtel 2002). Aussi, il est nécessaire de continuer à décrire les patterns de diversité, à des échelles locales comme régionales, chez tous les groupes, en tenant compte des autres composantes de la diversité pour réévaluer les patterns de diversité spécifique fréquemment décrits.

Encadré 2. Les arthropodes terrestres des forêts tropicales : pourquoi étudier les araignées ?

La plupart des espèces d'eukaryotes sont des arthropodes terrestres (Chapman 2009), et la plupart des arthropodes terrestres se trouvent dans les forêts tropicales (Erwin 1982). À bien des égards, les forêts tropicales représentent le biome le moins connus des diverses communautés peuplant les écosystèmes terrestres (Ramade 2003). Certains considèrent les forêts tropicales comme « la dernière frontière inexplorée de la biosphère » (Wilson 1992).

Les études ayant estimé la diversité des arthropodes tropicaux se basent sur la corrélation entre diversité spécifique des plantes et des animaux phytophages (e.g. Erwin 1982, Ødegaard 2000, Novotny *et al.* 2002). Or, les connaissances sur les relations entre diversité des plantes et des animaux non-phytophages (e.g. carnivores généralistes ou spécialistes, omnivores) sont lacunaires (mais voir Basset *et al.* 2012, Dinnage *et al.* 2012). Au sein des arthropodes, la plupart des groupes hyperdiversifiés semblent devoir leur diversité à une hyperdiversification des stratégies alimentaires (e.g. coléoptères, hyménoptères, lépidoptères, diptères, hémiptères et acariens sont des groupes polyphages) (Rainford & Mayhew 2015). Aussi, les estimations de la diversité des arthropodes tropicaux basées sur les relations plantes-animaux phytophages sont biaisées.

Parmi les groupes d'arthropodes hyperdiversifiés en forêt tropicale, les araignées forment l'un des seuls groupes à être exclusivement prédateur (Birkhofer & Wolters 2012). Étudier la diversité des araignées tropicales devrait donc permettre de tester les relations entre patterns de diversité des plantes et des arthropodes prédateurs.

Principaux processus responsables des patterns de diversité

La diversité actuelle est le produit de processus écologiques et évolutifs, pouvant être stochastiques (i.e. neutres) ou déterministes (i.e. liés à la niche), ainsi que de leurs interactions.

D'un point de vue des **processus écologiques déterministes**, des facteurs biotiques et abiotiques influencent les patterns de diversité (Weiher & Keddy 2001, Maire *et al.* 2012) via la différenciation de niche (MacArthur & Levins 1967) et le filtrage d'habitat (Keddy 1992), respectivement. Le filtrage d'habitat limite l'établissement des espèces qui ne sont pas capables de tolérer les conditions abiotiques d'un habitat donné, ce qui résulte en la survie d'espèces avec des attributs écologiques similaires dans un même endroit (Keddy 1992). Les interactions compétitives peuvent réduire la coexistence des espèces qui partagent des niches similaires (MacArthur & Levins 1967) ou renforcer les hiérarchies compétitives entre espèces (Chesson 2000, Kunstler *et al.* 2012), résultant en une différenciation des niches par le déplacement de caractères: par le partitionnement spatial et/ou temporel des espèces ayant des attributs écologiques similaires (Diamonds 1975, Gotelli & McCabe 2002). Ces processus déterministes s'appliquent à différentes échelles spatiales comme des échelles locales ou régionales (Chase & Myers 2011). Simultanément, les assemblages sont influencés par des **processus écologiques plus stochastiques** comme la colonisation, les extinctions aléatoires et la dérive écologique (Chase & Myers 2011).

Le rôle des **processus évolutifs** dans la détermination des patterns de diversité à l'échelle des assemblages a été moins étudié que celui des processus écologiques (Gillespie 2004). Un processus évolutif, la **radiation adaptative**, a été proposé comme le principal contributeur à la diversité de la planète (Simpson 1953, Schluter 2000). La radiation adaptative est un processus par lequel les organismes diversifient rapidement, à partir d'une espèce ancestrale, en une multitude de nouvelles formes écologiques différentes (Gillespie *et al.* 2001). C'est donc un processus complexe de spéciation dirigé par des facteurs écologiques (e.g. adaptation écologique) (Gavrilets & Vose 2005, Gillespie *et al.* 2020). Les radiations adaptatives les mieux connues proviennent des archipels isolés ou des pseudo-iles (e.g. lacs) (Gillespie *et al.* 2001) et sont souvent spectaculaires (e.g. les 15 espèces de pinsons des Galapagos, dits pinsons « de Darwin » (Lack 1983, Lamichhaney *et al.* 2015), les espèces de poissons Cichlidés des Lacs Tanganyika (208 espèces), Malawi (800-1000 espèces) et Victoria (plus de 200 espèces) en Afrique (Johnson *et al.* 1996, Galis & Metz 1998, Seehausen *et al.* 2008, Ronco *et al.* 2020), les environ 1000 espèces de Drosophilidae de l'archipel d'Hawaï (Carson & Kaneshiro 1976)).

Lier les patterns de diversité avec les processus à leur origine a été identifié comme l'un des grands défis de l'écologie (Vellend 2010). Le travail est colossal à l'échelle locale et les règles d'assemblages semblent si spécifiques (i.e. différents processus déterminent la diversité de différents taxons, et parfois entre contextes pour un même taxon) que certains parlent de la « boîte noire » de l'écologie des communautés pour désigner les liens entre patterns et processus (Vellend 2010), ainsi que le lien entre processus écologiques et évolutifs (Gillespie 2016).

Les trois principales composantes de la diversité

Les diversités en espèces, en traits et en unités évolutives sont liées. Nous détaillons dans cette partie ces trois composantes de la diversité et présentons l'intérêt de leur prise en compte de manière combinée pour déterminer les patterns de diversité.

L'approche taxonomique de la diversité

Les **espèces** comptent parmi les unités de base de la diversité et ont été longtemps considérées comme la composante la plus importante de celle-ci (Claridge *et al.* 1997, Hohenegger 2014). Cette importance est liée au fait que les espèces sont utilisées comme unité taxonomique de base en systématique (Linné 1735) et en biologie évolutive (Barraclough 2019). Elle a donc été pendant longtemps considérée comme le niveau fondamental en écologie (De Queiroz 2005). L'étude de la diversité spécifique des organismes a permis de mettre en évidence de nombreux patterns comme le gradient latitudinal de diversité, la relation aire-espèce, ou les successions le long de gradients environnementaux. Elle a l'avantage d'être facilement compréhensible et accessible si les espèces étudiées sont connues. Toutefois, l'approche diversité spécifique a aussi ses limites.

La première est liée à la difficulté **de définir et de délimiter les espèces**. Les biologistes ont, au cours de l'histoire, utilisé différents concepts d'espèce, dont certains partiellement incompatibles (Mayden 1997, De Queiroz 1998, 2007). Une définition unifiée et simplifiée a été proposée (Giray 1976, Dayrat 2005, De Queiroz 2007) dans laquelle les espèces sont « des lignées de population ou métapopulations qui évoluent séparément ». En tenant compte de cette définition, une approche intégrative de la délimitation d'espèce (taxonomie intégrative) a vu le jour prenant compte des critères de phylogéographie, morphologie comparative, génétique des populations, écologie, développement et comportement (Dayrat 2005). L'approche de taxonomie intégrative demande une bonne connaissance des organismes étudiés. Or ce n'est pas toujours le cas (e.g., les groupes d'arthropodes hyperdiversifiés des forêts tropicales ou des écosystèmes isolés), et il est alors nécessaire d'avoir recours à des approches de parataxonomie pour pouvoir estimer la diversité. Dans cette thèse, nous parlerons de diversité taxonomique.

Le deuxième problème que pose la diversité en espèces repose sur **les mesures de celle-ci**. La diversité spécifique est généralement représentée par la seule richesse spécifique: le nombre d'espèces (Humphries *et al.* 1995, Colwell 2009). Or la richesse spécifique est une mesure incomplète de la diversité spécifique, généralement faussée par l'incapacité des échantillonnages à collecter toutes les espèces d'un assemblage et par le fait que les espèces ne sont pas toutes aussi abondantes les unes que les autres (Chao, Gotelli, *et al.* 2014). Plusieurs solutions à ces problèmes ont été proposées et sont abordées dans l'**Encadré 3** (page 11).

Enfin, la **diversité spécifique** est une approche parfois **trop simpliste**. En effet, les mesures de diversité taxonomique reposent sur les hypothèses suivantes : (i) toutes les espèces sont égales, (ii) tous les individus sont égaux (quelle que soit leur taille), (iii) le nombre et l'abondance des espèces ont été correctement évalués avec des outils appropriés et dans des unités similaires (Magurran 2004). Cependant, aucune de ces hypothèses n'est valable car (i) les espèces ne sont pas égales dans leurs effets sur le fonctionnement de l'écosystème puisque leurs traits influencent les processus écosystémiques ; (ii) il existe une variation interindividuelle dans la façon dont les individus d'une même espèce utilisent les ressources (par exemple, pour les espèces généralistes : un individu peut surexploiter une des multiples ressources connues pour l'espèce) ; (iii) leur nombre et leur abondance sont généralement très sous-échantillonnés, et quasiment impossible à échantillonner de manière fiable. La diversité spécifique est donc peu représentative de la diversité, ce qui s'exprime notamment à travers le fait que les modèles testant les facteurs à l'origine des patterns de diversité spécifiques ne permettent pas de trancher entre les différents processus (e.g. perturbation, dispersion, gradients environnementaux et spatiaux, Chase *et al.*, 2005).

L'approche basée sur les traits

La **diversité fonctionnelle** (i.e. la composante fonctionnelle de la diversité) peut être définie comme « la valeur et la gamme des traits des espèces et organismes qui influencent le

fonctionnement de l'écosystème » (Tilman 2001). Mesurer la diversité fonctionnelle revient à mesurer la diversité des traits fonctionnels. Les traits sont, d'après Kattge *et al.* (2011) « des caractéristiques morphologiques, anatomiques, biochimiques, physiologiques ou phénologiques mesurables au niveau individuel (Violle *et al.* 2007) qui reflètent le résultat de processus d'évolution et d'assemblage de communautés répondant à des contraintes environnementales abiotiques et biotiques (Valladares *et al.* 2007) ».

L'approche fonctionnelle a été incorporée seulement récemment en écologie animale et pour les arthropodes terrestres (Pey *et al.* 2014, Moretti *et al.* 2017, Brousseau *et al.* 2018, Perović *et al.* 2018, Lowe *et al.* 2020). Bien que le terme « diversité fonctionnelle » soit largement utilisé et accepté, nous préférons utiliser les termes « diversité des traits » et « approche basée sur les traits » à moins que la fonctionnalité des traits ait été évaluée (en évaluant les relations entre les traits et la fitness le long de gradient environnementaux, voir Wong, Guénard, & Lewis, 2019). Or, en ce qui concerne la majorité des arthropodes terrestres, la fonctionnalité des traits n'a pas été explicitement testée (Wong *et al.* 2019).

En considérant les traits, et pas l'identité des espèces, il est possible de décrire de manière complémentaire les patterns de diversité en tenant compte de la niche occupée par les individus. La niche peut être définie comme l'ensemble de conditions environnementales, i.e. physiques (e.g. habitat, température, humidité, pH) et de ressources (e.g. type particulier de nourriture, taille de nourriture), dans lesquelles des populations stables peuvent se maintenir. Les individus et espèces co-existant dans une communauté sont alors sensés partager un ensemble de traits sélectionnés par les conditions environnementales. En prenant en compte l'information portée par les traits il est possible d'obtenir une meilleure compréhension des **processus écologiques** (déterministes vs. neutres) qui déterminent la diversité des communautés dans différentes conditions environnementales (McGill *et al.* 2006, Petchey & Gaston 2006, Mouchet *et al.* 2010, Webb *et al.* 2010, Leroy *et al.* 2014, Wong *et al.* 2019). Si les traits sont mesurés directement sur les individus, l'approche trait permet de prendre en compte à la fois la variation inter- et intraspécifique (Wong *et al.* 2019), des informations précieuses pour les études comparatives³ en écologie des communautés (Bolnick *et al.* 2011, Violle *et al.* 2012, Fontana *et al.* 2016).

Les traits sont aussi étudiés dans les reconstructions des morphologies ancestrales (Harmon *et al.* 2010) ou pour comprendre comment différents traits ont évolué entre différents clades phylogénétiques (Kuntner & Coddington 2020).

L'approche phylogénétique

La phylogénie s'intéresse à la détermination de l'histoire et des **relations évolutives** des organismes. Les relations sont supposées par des méthodes d'inférence phylogénétique qui évaluent les traits héréditaires observés (e.g. ADN, traits morphologiques) selon un modèle

³ D'après la définition de Paradis (2014), la méthode comparative est définie comme une approche analytique basée sur la comparaison de différents objets dans l'objectif d'élucider les mécanismes à l'origine de leur diversité.

spécifique d'évolution. L'histoire évolutive et les relations entre organismes sont le résultat de pressions de sélection du fait de processus écologiques et évolutifs (Mouquet *et al.* 2012) tels que le tri environnemental, l'exclusion compétitive, l'immigration et la spéciation (Gillespie 2004, Emerson & Gillespie 2008, Cavender-Bares *et al.* 2009). Aussi, la prise en compte de l'information phylogénétique nous informe sur les processus qui déterminent les patterns de diversité, que ce soit à l'échelle des lignées ou des communautés.

Plus récemment, l'information phylogénétique a été utilisée pour calculer des indices de diversité phylogénétique (voir Tucker *et al.*, 2017 pour une synthèse récente) et mieux comprendre la diversité des communautés. La diversité phylogénétique est calculée à partir des longueurs de branches d'un arbre phylogénétique, séparant les espèces d'une communauté. Cette approche se base sur l'hypothèse que le schéma de ramification d'un arbre phylogénétique reflète l'accumulation de différences phénotypiques, génétiques et comportementales entre les lignées évolutives. Et que ces différences accumulées peuvent décrire, expliquer ou prédire les processus évolutifs et écologiques à l'origine de l'assemblage des communautés (Tucker *et al.* 2017).

La diversité phylogénétique a été considérée pendant un temps comme un proxy de la diversité fonctionnelle (Prinzing *et al.* 2001, Webb *et al.* 2002, Cavender-Bares *et al.* 2009). Il a depuis été montré que l'information phylogénétique n'est pas un proxy de l'information portée par les traits (notamment du fait de la convergence évolutive⁴ et du conservatisme phylogénétique de niche⁵) et qu'elle lui est complémentaire pour notre compréhension de la diversité et des règles d'assemblages des communautés (Cadotte *et al.* 2013, Pavoine *et al.* 2013, Gerhold *et al.* 2015, Hacala *et al.* 2021, Ridel *et al.* 2021).

Combiner l'étude des principales composantes de la diversité

Les diversités en unités taxonomiques, en traits et en unités évolutives sont liées. Les organismes interagissent sur la base de ces traits, ce qui détermine les modèles de coexistence des espèces (Tilman *et al.* 2014). Les traits sont quant à eux déterminés par les origines évolutives des organismes et l'environnement dans lequel ils évoluent.

Pavoine & Bonsall (2011) ont montré que la comparaison de la diversité phylogénétique avec la diversité des espèces (ou taxons) peut révéler des processus historiques, notamment une radiation adaptative récente, des taux d'immigration élevés, des différences dans les taux de spéciation et l'expansion des aires de répartition entre les lignées. Ils ont aussi montré que la combinaison de la diversité phylogénétique et de la diversité des traits peut être utilisée pour démêler les hypothèses sur les processus historiques et biogéographiques par rapport

⁴ La convergence évolutive est le résultat de mécanismes évolutifs ayant conduit des espèces, soumises aux mêmes contraintes environnementales (niches écologiques similaires), à adopter indépendamment plusieurs traits physiologiques, morphologiques ou comportementaux semblables (e.g. apparition des nageoires chez les poissons, les mammifères aquatiques et les oiseaux marins [aile d'un point de vue morphologique, nageoire d'un point de vue fonctionnel])

⁵ Le conservatisme phylogénétique de niche correspond à la tendance des lignées à conserver, au cours du temps et de l'évolution, leur niche écologique et les traits écologiques associés

aux processus écologiques dans la détermination des compositions en espèces des communautés et des régions. Aussi, combiner l'approche phylogénétique avec les analyses de diversité taxonomique et de diversité des traits permet de mieux décrire les patterns de diversité et les processus à leur origine. Cette approche unifiée (Figure 2) est prometteuse et a fait ses preuves sur de nombreux groupes comme les plantes (Pavoine *et al.* 2011, Zhang *et al.* 2020), le zooplancton (Gianuca *et al.* 2017), les papillons (Pavoine *et al.* 2014) ou les crevettes (Head *et al.* 2018).

Afin de pouvoir combiner ces trois composantes de la diversité, il est nécessaire d'avoir des connaissances fiables à la fois sur la taxonomie, les traits (et leur fonctionnalité) et la phylogénie du groupe étudié. Cela passe dans un premier temps par la description des taxons, l'étude des traits et la construction de phylogénies. Toutefois, pour certains groupes d'intérêt comme les arthropodes terrestres tropicaux, nous n'avons pas accès à ces connaissances de bases (Fichaux *et al.* 2019) et il est nécessaire de consacrer de l'effort de recherche à celles-ci (e.g. description d'espèces, mesures de traits sur les individus, détermination des phylogénies). Une fois ces informations acquises, il est nécessaire d'avoir recours à des mesures fiables et comparables des diversités de chacune de ces composantes.

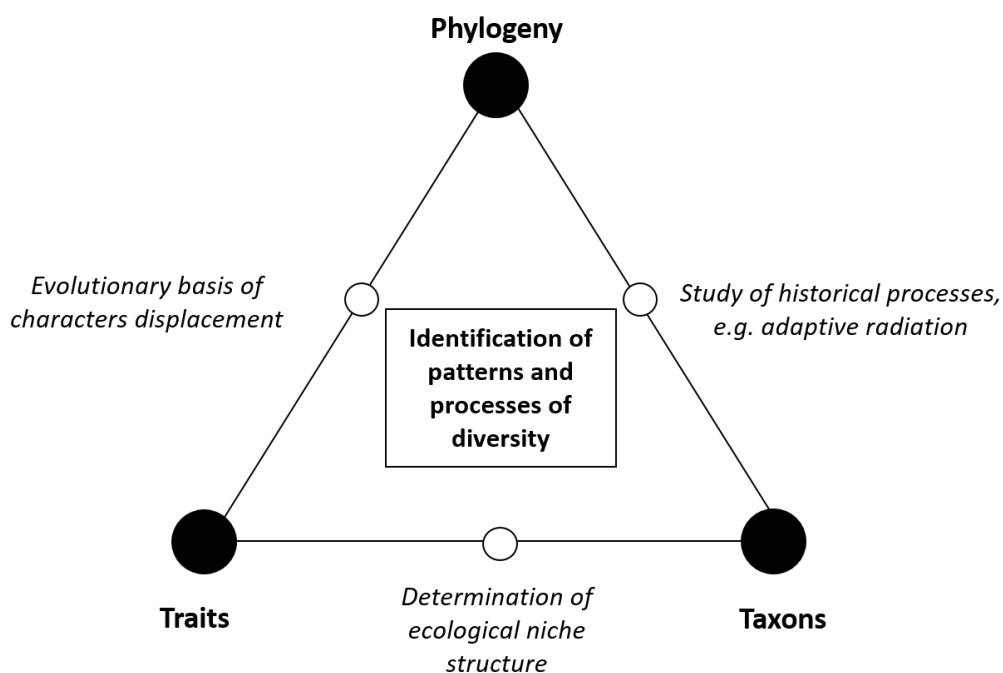


Figure 2: Schéma synthétisant les apports de la combinaison des taxons, traits et des phylogénies dans l'identification des patterns et la compréhension des processus à l'origine de la diversité. En étudiant les patterns de diversité phylogénétique on peut prendre en compte les processus historiques et évolutifs dans l'assemblage des communautés. Étudier les patterns de diversité taxonomique et de traits en même temps permet de déterminer la structure de la niche écologique. Prendre en compte la phylogénie dans les études de traits permet de tenir compte de la base évolutive du déplacement de caractère à l'origine des traits observés. Inspiré d'un schéma de Webb et al. 2002 sur les approches intégrant la phylogénie, les traits et les communautés.

Encadré 3. Mesurer la diversité

Les patterns de diversité observés, et donc les inférences sur les processus à leur origine, dépendent des méthodes d'étude et d'échantillonnage. Dans cette partie nous présentons les paramètres et étapes clés pour mesurer la diversité et décrire ses patterns de manière fiable et le plus précisément possible : les échantillonnages ainsi que les mesures de la diversité.

L'échantillonnage de la diversité – La première étape pour une détermination précise de la diversité repose sur un échantillonnage standardisé des organismes cibles. La standardisation des échantillonnages permet une comparaison plus fiables des assemblages, et est préférée au échantillonnage *ad-hoc*, même si ceux-ci peuvent être localement plus efficaces (Cardoso *et al.* 2009). Malumbres-Olarte *et al.* (2017) définissent les échantillonnages standardisés comme un compromis de sept critères : (1) l'efficacité (rendement), qui dépend de l'intensité d'échantillonnage, (2) l'adéquation au taxon et/ou à la question posée, qui dépend notamment des méthodes employées, (3) la comparabilité entre sites, habitats ou biomes par exemple, même si le protocole est sous-optimal pour chaque site, (4) la faisabilité (compte tenu des ressources), (5) la flexibilité, (6) la transparence (afin d'être reproductible) et (7) la fiabilité. L'utilisation de tels protocoles est particulièrement importante pour les études sur les groupes d'organismes hyperdiversifiés comme les arthropodes terrestres. Pourtant, les protocoles standardisés ont été relativement rarement utilisés et peu de données comparables existent sur leur diversité (Cardoso, Erwin, *et al.* 2011) (voir section **Les difficultés de l'étude de la diversité des araignées tropicales**, page 22 et suivantes).

Les mesures de la diversité – À l'exception des groupes d'organismes très bien connus dans des endroits eux-mêmes très bien connus, les échantillonnages sont en général biaisés par les organismes non détectés (Coddington *et al.* 2009). La plupart des assemblages contiennent des espèces rares et la taille des assemblages varient entre habitats (Chao & Jost 2012, Chao, Gotelli, *et al.* 2014). Aussi, même si l'on échantillonne les assemblages de manière standardisée, avec une intensité d'échantillonnage suffisante, les échantillonnages sont souvent incomplets et l'on sous-estime la diversité. Afin de pouvoir faire des comparaisons standardisées de la diversité entre assemblages, il est alors nécessaires d'avoir recours à des méthodes d'estimation de la diversité (Gotelli & Colwell 2001, Chao, Gotelli, *et al.* 2014) et de la comparer à un même niveau de complétude d'échantillonnage (Jost 2010, Chao & Jost 2012, Chao, Gotelli, *et al.* 2014). Historiquement, les comparaisons des diversités estimées ont été réalisées à une même taille d'échantillon. Hors la taille d'échantillon ne tient pas compte du fait que certains assemblages sont plus riches que d'autres, et mène donc à une sous-estimation des grands assemblages (Chao & Jost 2012). La complétude d'échantillonnage représente quant à elle la proportion d'espèce de l'assemblage représentées dans un échantillon (Chao & Jost 2012). Comparer les diversités estimées des assemblages sur la base de la complétude tient compte du fait que des assemblages plus divers nécessitent un plus gros effort d'échantillonnage afin d'être correctement caractérisés (voir Roswell, Dushoff, & Winfree, 2021 pour une revue à ce sujet).

Il existe d'autre part une myriade de mesures possibles de diversité, qui ne tiennent pas tous compte des mêmes informations. Trois grandes catégories d'information portées par ces indices ont été identifiées : la richesse, la régularité et la divergence (Magurran 2004, Mouillot *et al.* 2005, Ricotta 2007, Pavoine & Bonsall 2011, Chao, Chiu, *et al.* 2014). La **richesse** désigne le nombre d'unités de diversité, que ce soit les espèces (ou taxons), les traits ou les unités évolutives. La **régularité** prend elle est compte la distribution des abondances entre les unités de diversité et déterminent si celle-ci sont distribuées de manière équitable (Mouillot *et al.* 2005). La **divergence** quant à elle correspond à une mesure de la dissimilarité entre organismes, calculée à partir des distances taxonomiques, en traits ou des distances phylogénétiques. Les différents indices existants varient dans leur prise en compte de ces trois types d'information et peuvent conduire à des observations différentes de la diversité des assemblages (Liu *et al.* 2007). L'utilisation d'une seule mesure de la diversité est donc insuffisante pour avoir une bonne représentation de celle-ci et il est préférable d'utiliser un ensemble d'indices de diversité en même temps (Liu *et al.* 2007). Des **mesures unifiées des trois catégories d'information** sur la diversité (richesse, régularité et divergence) ainsi que des trois composantes de la diversité (taxonomique, traits, unités évolutives) permettent en conséquence d'avoir une vision plus complète de la diversité (Pavoine & Bonsall, 2011; voir notamment l'utilisation des nombres de Hill par Chao *et al.*, 2014a, 2014b).

Les araignées comme modèle pour l'étude de la diversité

Les araignées (Araneae) ont été identifiées comme groupe modèle pour étudier les patterns de diversité et les processus à leur origine (Cardoso, Pekár, *et al.* 2011, Birkhofer & Wolters 2012, Malumbres-Olarte *et al.* 2018). Pourtant, les connaissances sur leurs diversités restent faibles. Nous synthétisons dans cette partie les aspects de la diversité des araignées importants pour cette thèse.

Le succès évolutif et écologique des araignées

Les araignées sont considérées par beaucoup de chercheurs comme un groupe à succès (e.g. Bond & Opell, 1998; Blackledge, Coddington, & Gillespie, 2003; Kuntner & Agnarsson, 2011; Dimitrov & Hormiga, 2021). Certains parlent de succès écologique, d'autres de succès évolutif, sans vraiment les définir (mais voir Dimitrov & Hormiga, 2021).

Le succès biologique est un concept datant de la moitié du 19^e siècle qui a le plus souvent été discuté en terme de comparaison entre groupes d'organismes, à des niveaux taxonomiques ou non, mais toujours à un niveau plus élevé que celui d'espèce (Wasik & Turner 2013). Nous avons identifié, dans la littérature, cinq caractéristiques constantes dans la notion de succès biologique : (1) la diversité, (2) la longue histoire évolutive, (3) la présence d'innovations clés propres au taxon (que nous regrouperons sous le terme de succès évolutifs) ainsi que (4) l'ubiquité écologique et (5) l'abondance (que nous regrouperont sous le terme de succès écologique). Les araignées répondent à ces cinq caractéristiques :

- (1) Les araignées font partie des **arthropodes terrestres les plus diversifiés** (Wheeler *et al.* 2017) avec plus de 49 600 espèces décrites (World Spider Catalog 2021). On estime que la diversité totale des araignées devrait se situer entre 76 000 et 170 000 espèces (Coddington & Levi 1991, Platnick & Raven 2013). Parmi les chélicérates, les araignées dénotent par leur extrême diversité (**Figure 3**). Elles présentent par exemple 74 fois plus d'espèces décrites que leur clade frère, les Pédipalpis.
- (2) Les araignées forment un **taxon ancien**, dont la longue histoire de diversification a surpassé les extinctions. Leurs racines sont estimées vieilles de 400 millions d'années (Dévonien moyen, Coddington & Levi, 1991; Fernández *et al.*, 2018). Les ancêtres des arachnides (groupe composé entre autres des araignées, scorpions, tiques, opilions, voir **Figure 3**) vivaient probablement en milieu aquatique (Roy *et al.* 2015) (voir **Figure 3** les Pycnogonides qui sont un groupe aquatique). Par conséquent, les araignées pourraient avoir été parmi les premiers animaux à vivre sur terre (Selden & Penney 2010), plus de 150 millions d'années avant les dinosaures.

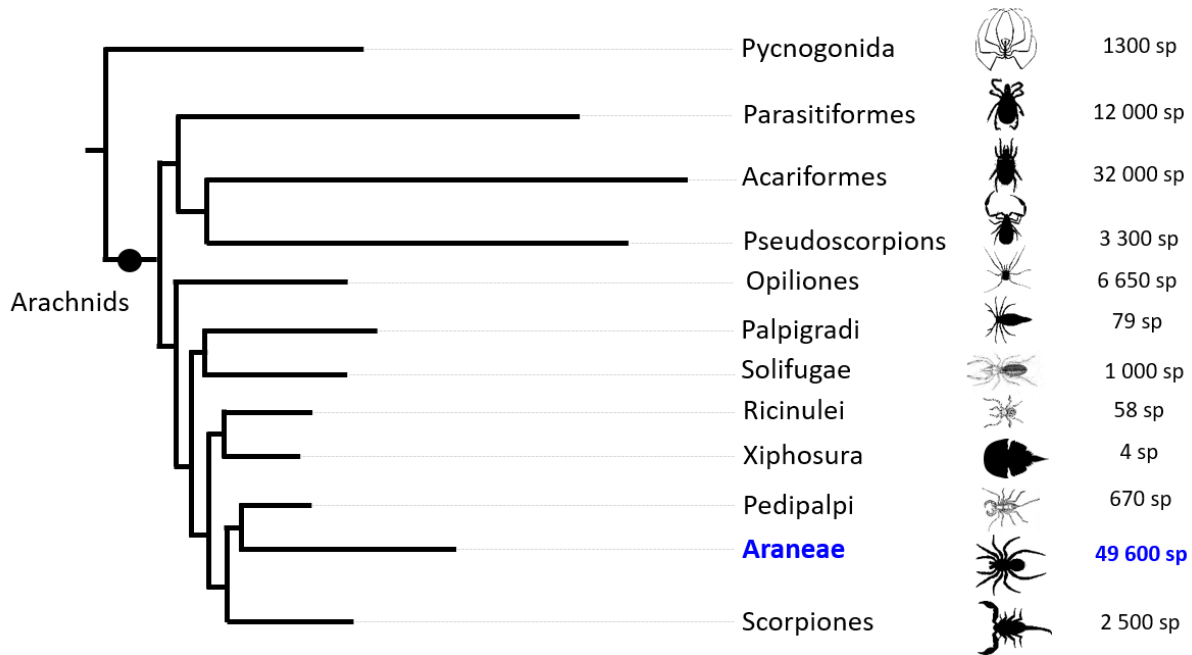


Figure 3 : Schéma représentatif de l'arbre des Chelicerates et de leur diversité, produit en reprenant la topologie de l'arbre des Chelicerates de Ballesteros et al. (2019). Les longueurs de branche ne sont pas à l'échelle.

- (3) Les araignées présentent un ensemble **d'innovations clés** propre à leur groupe comme leur filières (organes producteurs de soies), leur système respiratoire par trachée, leur système sensoriel (poils et fentes répartis sur une grande partie de leur corps), leurs diverses utilisations de la soie, dont les différents types de toiles, leur capacité à produire du venin ainsi que leurs différents comportements de chasse (voir Dimitrov et Hormiga, 2021 pour une revue détaillée).
- (4) L'**écologie** des araignées est remarquable de par leur distribution, leur affinité d'habitats, et leur rôle de prédatrice. En effet, les araignées sont **distribuées sur toute la surface de la planète**, sauf en Antarctique (Natural Environmental Research Council 2012). On trouve des araignées dans **tous les écosystèmes terrestres** (Turnbull 1973), des îles arctiques jusqu'aux régions désertiques, dans les zones de végétation riche mais aussi dans des environnements pauvres comme les grottes, les zones intertidales et le sommets des montagnes et volcans (Foelix 2010). Malgré leur large distribution, les araignées ont souvent une **affinité d'habitat très spécifique** (Foelix 2010) et vivent dans des environnements bien définis. Les limites de ces environnements sont déterminées par des facteurs abiotiques (température, humidité, structure de la végétation) et des facteurs biotiques (ressources disponibles, compétiteurs, ennemis). En conséquence, les espèces d'araignées s'échelonnent en général en accord avec les strates de la végétation (Foelix 2010). Dans tous ces habitats, les araignées sont le **principal groupe de prédateurs** (Pekár *et al.* 2017). En effet, les araignées sont toutes exclusivement prédatrices (Meehan *et al.* 2009, Nyffeler & Birkhofer 2017) et principalement généralistes (Pekár *et al.* 2012, Pekár & Toft 2015). Contrairement aux autres groupes d'arthropodes hyperdiversifiés (e.g., Coléoptères, Hyménoptères, Lépidoptères, Diptères, Hémiptères et Acariens), la diversification

évolutive des araignées n'est pas le résultat de la diversification des régimes alimentaires (Rainford & Mayhew 2015). Elles présentent cependant un grand nombre de stratégies alimentaires.

- (5) Les araignées sont **un des groupes les plus abondants** (Turnbull 1973, Coddington & Levi 1991, Nyffeler & Birkhofer 2017). Leur densité a été estimée à une moyenne de 131 araignées par m² sur différentes zones du globe (Turnbull 1973), et jusqu'à 1000 araignées par m² dans des conditions favorables (Ellenberg *et al.* 1986).

Taxonomie des araignées

Avec 49 600 espèces décrites sur 76 000 à 170 000 espèces potentielles d'araignées (Coddington & Levi 1991, Platnick & Raven 2013, World Spider Catalog 2021), on ne connaît même pas la moitié des espèces. La taxonomie des araignées (découverte et description d'espèces) est pourtant un domaine considéré comme actif (Agnarsson *et al.* 2013) qui semble résister à « l'obstacle taxonomique » ou « taxonomic impediment » (Rodman & Cody 2003, Engel *et al.* 2021, Jäger *et al.* 2021), avec par exemple un total de 500 nouvelles espèces décrites entre 2003 et 2013 (Agnarsson *et al.* 2013). La communauté des arachnologues s'est notamment attaqué à la question fastidieuse de la synonymie (i.e. description sous des noms différents de la même espèce par différents taxonomistes, biaisant donc les estimations de la diversité) en plaçant la liste et les décisions taxonomiques dans le domaine public sur le site du World Spider Catalog (World Spider Catalog 2021). Comme chez les autres groupes peu connus mais extrêmement diversifiés, le principal facteur limitant le développement de la taxonomie des araignées est le nombre d'arachnologues pour les découvrir et les étudier (Platnick 1991, Foord *et al.* 2011, Agnarsson *et al.* 2013). On ne peut toutefois pas attendre que toutes les espèces soient décrites pour étudier les patterns de diversité taxonomique. Aussi, des approches de parataxonomies sont utilisées pour étudier la diversité des assemblages dont les araignées ne sont pas connues (voir la section Travailler avec des espèces inconnues pages 22-23).

État de l'approche basée sur les traits chez les araignées

Les patterns de diversité en traits des araignées n'ont pas été aussi largement étudiés que ceux de leur diversité taxonomique (Gallé *et al.* 2017). Les traits ont été utilisés pendant longtemps comme principal critère en phylogénie des araignées (Agnarsson *et al.* 2013). Toutefois, l'étude des relations entre traits et gradients environnementaux, dans le but de déterminer les processus responsables des assemblages remonte elle seulement à une 15^{aine} d'années (**Encadré 4**).

Cette approche est donc relativement récente chez les araignées et manque encore d'un cadre commun (e.g. mesures communes, voir **Encadré 4**). La fonctionnalité des traits n'a pas été testée chez les araignées (comme chez la plupart des arthropodes terrestres, Wong *et al.* 2019 mais voir Moya-Laraño *et al.* 2013). Aussi, de traits nombreux traits sont étudiés (**Encadré 4**), sans que l'on puisse être certain du lien de ceux-ci avec les variables

environnementales. Au sein de cette multitude de traits, les plus utilisés sont les guildes de chasses et la taille du corps (**Encadré 5**).

Encadré 4. L'approche diversité des traits dans les études sur les assemblages des araignées

À titre exploratoire, nous avons revu les études publiées sur l'approche diversité des traits chez les araignées par une requête sur World of Science avec les mots « trait », « spider* » et « fonction* » en avril 2019. Nous avons identifié 83 études publiées entre 2008 et 2019 portant sur la diversité des traits dans un contexte d'étude des processus à l'origine des assemblages d'araignées.

59 traits différents ont été utilisés dans ces études, que l'on peut classer en 7 catégories (**Figure 4**) : traits comportementaux, alimentaires, propriétés environnementales, traits d'histoire de vie, traits morphologiques, phénologiques, et physiologiques. Certains traits font partie de plusieurs catégories à la fois. Les 10 traits les plus abondants sont listés dans le **Tableau 1**. Les principales catégories de traits utilisées sont des traits comportementaux et alimentaire, ainsi que des traits morphologiques et parmi eux les traits guildes de chasse et taille du corps, respectivement (confirmé par Pekar et al. accepté : **Annexe 2**).

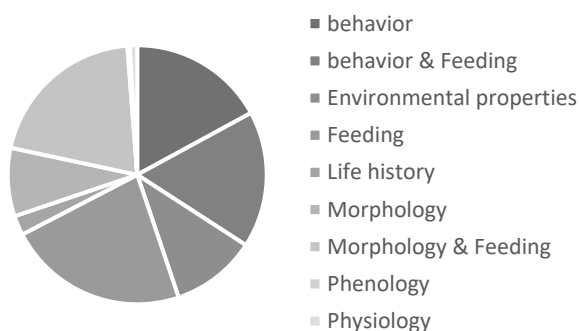


Figure 4: Catégories des traits utilisés dans les études sur les araignées

Table 1: 10 principaux traits étudiés chez les araignées et leur représentativité dans les 83 études revues pour cette analyse.

Trait	Representativity
Body size	20%
Hunting guilds	18%
Dispersal ability	9%
Habitat preference	9%
Circadian activity	5%
Abiotic preference	4%
Diet specialization	4%
Phenology	2%
Leg size	2%
Eye size	1%

On remarque aussi que les mesures d'un même trait peuvent varier entre étude. À titre d'exemple, le trait taille du corps peut être la longueur totale moyenne de l'araignées (e.g. Ricotta *et al.*, 2011; Simons, Weisser, & Gossner, 2016; Schirmel *et al.*, 2016; Braaker *et al.*, 2017; Rigal *et al.*, 2018; Gallé *et al.*, 2018, 2019; Nagy *et al.*, 2018; Fernandez-Fournier *et al.*, 2018; Joseph *et al.*, 2018; Buchholz *et al.*, 2018; Turney & Buddle, 2019), seulement chez les femelles (e.g. Lambeets *et al.*, 2009; Gomes, Carvalho, & Gomes, 2018), la longueur totale et celle de l'opisthosome (e.g. Gibb *et al.*, 2015), la longueur du prosome (e.g. Langlands *et al.*, 2011), la longueur et la largeur du prosome (Puzin *et al.* 2014, Lafage *et al.* 2015, Penell *et al.* 2018, Pétilion *et al.* 2018), la largeur du prosome seule (e.g. Dahirel *et al.*, 2017), le ratio entre la largeur et la longueur du sternum (e.g. Mammola *et al.*, 2018).

Le nombre important de traits et de mesures possibles laisse entrevoir qu'il n'y a pas d'approche commune ni de consensus sur les traits à utiliser pour résoudre les questions portant sur l'assemblage des assemblages d'araignées.

Parmi ces 83 études, plus de la moitié se sont intéressées à des traits qu'ils ont extraits de la littérature (**Figure 5**). Cela met en évidence la pratique la plus courante des études sur la diversité en trait des assemblages d'araignées qui est d'aller chercher des valeurs de traits dans la littérature existante. La compilation des valeurs des traits pour les espèces des assemblages est alors un travail laborieux car, pour certains traits et pour certaines espèces, l'information n'existe pas ou n'est pas facilement accessible car cachée dans d'anciennes publications ou dans des travaux non publiés (Moya-Laraño *et al.* 2013). Cette tendance à se baser sur les traits issus de la littérature reflète le fait que la plupart des études ont été menée en Europe (principalement Allemagne, France, Belgique, République Tchèque) (confirmé par Pekar et al. accepté : **Annexe 2**) dans des milieux bien étudiés (forêts et prairies) pour lesquels les informations sont plus facilement accessibles à partir de la littérature.

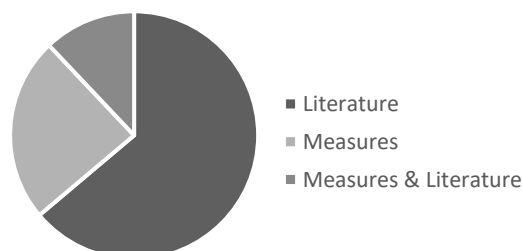


Figure 5: Sources des traits utilisés dans les études sur les araignées

Si une classification des guildes de chasse a été proposée et plusieurs fois revue (Uetz 1977, Uetz *et al.* 1999, Cardoso, Pekár, *et al.* 2011), aucune règle de mesure de la taille du corps n'a été édictée pour les études reliant traits et gradients environnementaux (mais voir Jakob, Marshall, & Uetz, 1996 pour une mesure dans le cadre des études sur la fitness), si bien que les différentes études qui s'y intéressent utilisent différentes mesures (**Encadré 4**). De plus, la taille du corps est un trait difficile à relier à un filtre en particulier car elle est corrélée à plusieurs types de facteurs (Brousseau *et al.* 2018) (e.g. métaboliques (Brown *et al.* 2004 in Brousseau et Gillooly *et al.* 2001)), physiologiques (e.g. privation de nourriture, résistance à la dessiccation), environnementaux (e.g. températures, utilisation des ressources, vulnérabilité aux ennemis naturels) (Cushman *et al.* 1993, Entling *et al.* 2010). Enfin, l'approche basée sur les traits telle qu'elle a été employée ces 15 dernières années repose majoritairement sur des traits issus de la littérature (**Encadré 4**), ce qui a pour avantage d'être plus facilement accessible que de devoir effectuer un ensemble de mesures sur de nombreux individus mais se limite aux informations présentes dans la littérature et ne tient pas compte de la variabilité intra-spécifique.

Encadré 5. Les guildes de chasse des araignées

Des **guildes d'araignées** regroupant les espèces qui utilisent les mêmes ressources de manière similaires (e.g. proies, habitats) (Blondel 2003), et reflétant donc leur niche écologique, ont été déterminées. Bien que de nombreuses classifications de guildes existent, la principale utilisée est celle basée sur les stratégies alimentaires (Cardoso, Pekár, *et al.* 2011), aussi appelées guildes de chasse.

Les guildes de chasse sont définies à l'échelle des familles, en faisant l'hypothèse que celles-ci sont conservées à l'échelle de la famille (Cardoso, Pekár, *et al.* 2011). On classe généralement les guildes de chasse en huit catégories (Uetz *et al.* 1999, Dias *et al.* 2009, Cardoso, Pekár, *et al.* 2011) allant des différentes techniques de construction de toile – (1) les tisseuses de toile de détection (sensing web weavers), (2) les tisseuses de toile en nappe (sheet web weavers), (3) les tisseuses de toiles spatiales (space web weavers) et (4) les tisseuses de toile orbitale (orb web weavers) – aux techniques de chasse des araignées errantes – (5) les chasseuses en embuscades, (6) les chasseuses au sol et (7) les autres chasseuses – jusqu'aux (8) spécialistes. Comme les membres d'une même guildes peuvent avoir des rôles fonctionnels similaires dans les communautés, les guildes de chasse des araignées sont été considérés comme des groupes fonctionnels.

Le conservatisme de la guildes de chasse à l'échelle des familles a été remis en question (Dias *et al.* 2009, Suter & Benson 2014) et certaines classifications prennent en compte le fait que différentes stratégies alimentaires puissent être utilisées au sein d'une même famille d'araignée (e.g. Dias *et al.* 2009).

L'approche basée sur les traits chez les araignées a pris un nouveau tournant lors d'un workshop qui s'est tenu à Christchurch (Nouvelle-Zélande) en 2019 intitulé « Spider trait network : opportunities for a global collaboration to address broad scale ecological and evolutionary questions ». Ce workshop a permis d'identifier les enjeux de la création d'une base de traits dédiée aux araignées, synthétisés par Lowe *et al.* (2020) (Annexe 1), et d'initier sa création. Lowe *et al.* (2020) rappellent la nécessité de créer une base de données mondiale des traits sur les araignées afin d'unifier nos données (i.e. utiliser les mêmes terminologies et les mêmes mesures) et d'améliorer l'efficacité et la reproductibilité des études utilisant les traits. Ils posent les bases d'une telle base de données en définissant les traits, leur normalisation, les types de données acceptées et la gouvernance d'une telle base. La **World Spider Trait database** (Pekár, Černecká, *et al.* 2021, Pekár, Wolff, *et al.* 2021, Appendix 2) a vu le jour en 2021. Celle-ci participe à la construction d'un cadre général d'étude des traits. Elle permettra, dans les années à venir, de déterminer la fonctionnalité des traits et de répondre à de nombreuses questions en macro-écologie, biogéographie et évolution par l'étude des patterns de diversité fonctionnelle à des échelles spatiales et temporelles larges et des relations entre diversité des traits et diversité phylogénétique. Il sera alors possible de déterminer à larges échelles la contribution relative des filtres environnementaux, de la dispersion et de l'exclusion compétitive dans la structuration des patterns de diversité spécifique et en traits des araignées.

Phylogénie des araignées

L'arbre phylogénétique des araignées commence lui tout juste à s'éclaircir (voir Figure 6 pour la topographie actuellement acceptée) grâce aux travaux menés ces dernières années (Dimitrov *et al.* 2011, Garrison *et al.* 2016, Wheeler *et al.* 2017, Fernández *et al.* 2018, Kulkarni *et al.* 2020, Kallal *et al.* 2021).

Les recherches sur les araignées ont été plutôt lentes à intégrer des approches de phylogénie moléculaire, commençant par quelques études dans les années 1990 (e.g. Gillespie, Croom, & Palumbi, 1994; Gillespie, Croom, & Hasty, 1997; Zehethofer & Sturmbauer, 1998). Les études de phylogénie moléculaire ont proliféré depuis mais notre compréhension de l'arbre des araignées et des relations fondamentales entre familles et espèces a été grandement ralentit par l'inadéquation des marqueurs moléculaires disponibles pour résoudre ces questions chez les araignées (e.g. 12S chez Lycosidae (Vink *et al.* 2002), 18S (Krehenwinkel *et al.* 2018), 28S (Murphy *et al.* 2006)). L'avènement des technologies de Next Generation Sequencing (NGS) et le développement des approches de phylogénomique et de transcriptomique a permis de résoudre les relations de base de l'arbre des araignées (Agnarsson *et al.* 2013, Brewer *et al.* 2015, Garrison *et al.* 2016, Garb *et al.* 2018, Kallal *et al.* 2021).

Des pans entiers de l'arbre des araignées restent toutefois encore peu étudiés. Par exemple, les relations entre les araignées lous (famille appartenant au clade RTA et l'une des plus diversifiées, World Spider Catalog, 2021) restent encore aujourd'hui peu comprises (mais voir Piacentini & Ramírez, 2019). La famille des araignées lous a donc été pointée comme l'une des priorités des futures recherches phylogénétiques sur les araignées à l'échelle mondiale (Garb *et al.* 2018).

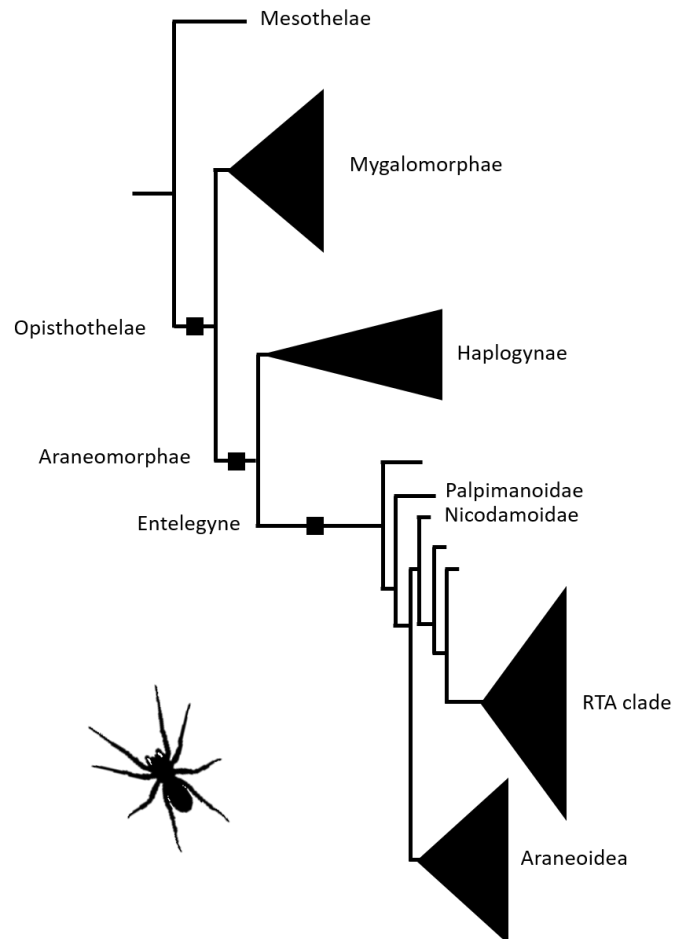


Figure 6 : Schéma représentatif de l'arbre des araignées représentant les principales grandes lignées identifiées à ce jour. RTA signifie retrolateral apophysis. Version schématique et simplifiée des arbres produits par Kulkarni *et al.* 2020. Les longueurs de branches ne sont pas à l'échelle.

En conséquence, peu d'études se sont intéressées à la diversité phylogénétique (confirmée par l'ADN) pour déterminer les patterns de diversité des assemblages d'araignées et les processus à leur origine (Ulrich *et al.* 2010, Cardoso 2012, Dolson *et al.* 2020, Hacala *et al.* 2021, Ridel *et al.* 2021). Du fait du manque de connaissance sur la phylogénie des araignées, ces études ont déterminé la diversité phylogénétique soit en se basant sur la classification taxonomique, en faisant l'hypothèse que la classification taxonomique reflète les relations phylogénétiques (Ulrich *et al.* 2010, Cardoso 2012), en combinant les arbres phylogénétiques avec la classification taxonomique (Hacala *et al.* 2021, Ridel *et al.* 2021).

Patterns de diversité et processus connus chez les araignées

La **diversité est distribuée de manière très inégale au sein des principales lignées d'araignées (voir lignées Figure 6)**. Par exemple, on dénombre environ 3 000 espèces au sein de la lignée des Mygalomorphes, contre plus de 46 000 chez les Araneomorphes, soit plus de 90% des toutes les espèces connues. Les Araneomorphes contiennent donc plus de 15 fois plus d'espèces que leur groupe frère du même âge géologique, les Mygalomorphes. Ce déséquilibre a mené à la formulation de plusieurs hypothèses sur les **processus responsables de la diversification** des araignées, revues par Dimitrov & Hormiga (2021). Par une synthèse des travaux récents, ces auteurs (1) montrent que l'importance des facteurs traditionnellement considérés comme principaux responsables de la diversification des araignées : co-diversification avec les insectes, rôle de la soie, de l'architecture des toiles et de la perte des toiles alimentaires, est moindre ; et (2) suggèrent que des facteurs moins explorés comme l'hétérogénéité environnementale, la sélection sexuelle, l'architecture du génome ou le microbiome ont pu jouer un rôle important dans la diversification des araignées. Les études menées sur les radiations d'araignées mettent en évidence que **les patterns de diversification varient grandement entre lignées** (Gillespie 2016) avec certaines lignées caractérisées par une faible différenciation écologique, et d'autres par une différenciation écologique forte. Par exemple, sur l'archipel d'Hawaii les *Tetragnatha* (Tetragnathidae) et les *Ariamnes* (Linyphiidae) présentent des épisodes répétés de différenciation écologique (Gillespie 1991, 2013, Blackledge *et al.* 2003, Blackledge & Gillespie 2004, Gillespie & Rivera 2007, Gillespie *et al.* 2018). A l'inverse, les *Orsonwelles* (Linyphiidae) ont toutes des écologies similaires (Hormiga *et al.* 2003).

Comme pour la plupart des organismes terrestres, on trouve chez les araignées **un gradient latitudinal de diversité spécifique** avec les assemblages les plus diversifiés trouvés dans les **écosystèmes tropicaux** (Santos *et al.* 2017, Piel 2018). Ce pattern n'est cependant pas retrouvé pour la diversité en traits, Cardoso *et al.* (2011b) ayant montré que la richesse en traits n'était pas toujours supérieure dans les régions tropicales par rapport aux régions tempérées. Les études des patterns de diversité des araignées à grandes échelles sont toutefois limitées par la seule disponibilité de données grossière à ces échelles du fait du manque de connaissance sur la diversité des araignées (Dimitrov & Hormiga 2021).

Aussi, la plupart des recherches sur les patterns de diversité des araignées consistent en des études à échelle locale et régionale de la diversité spécifique alpha et bêta (e.g. Yanoviak, Kragh, & Nadkarni, 2003; Entling *et al.*, 2007; Hore & Uniyal, 2008; Baldissera, Rodrigues, & Hartz, 2012; Barton *et al.*, 2017). Ces études mettent en évidence des **relations entre la richesse spécifique des araignées et les variables environnementales**, avec par exemple un nombre plus élevé d'espèces dans des habitats à la structure plus complexe (Greenstone 1984, Yanoviak *et al.* 2003, Entling *et al.* 2007, Baldissera *et al.* 2012, Ávila *et al.* 2017), une diversité différente entre micro-habitats (e.g. Whitehouse *et al.*, 2002; Barton *et al.*, 2017) et végétation (e.g. Hore & Uniyal, 2008). Des études prenant en compte les traits, il ressort que la diversité en trait des araignées est influencée par le type d'habitat et sa structure (e.g. Schirmel, Blindow, & Buchholz, 2012; Corcuera *et al.*, 2016). Les quelques études disponibles sur la diversité phylogénétique des araignées (Ulrich *et al.* 2010, Cardoso 2012, Cardoso *et al.* 2014, Dolson *et al.* 2020, Hacala *et al.* 2021, Ridel *et al.* 2021, Steinke *et al.* 2021) ont aussi montré que la diversité de leurs assemblages était contrainte par des filtres environnementaux. De plus, au sein des arthropodes terrestres, les assemblages d'araignées semblent être plus structurées par les variables environnementales et moins par la compétition que ceux d'autres taxons dominant la macro-arthropofaune terrestre du sol comme les carabes ou les fourmis (Wise 2006, Fichaux *et al.* 2019, Hacala *et al.* 2021)

Les variables environnementales liées à l'habitat semblent donc avoir un rôle important dans la structuration de la diversité des assemblages d'araignées.

Étude de la diversité des araignées en milieux tropicaux

Milieux tropicaux : hauts lieux de diversité

Les milieux tropicaux sont les écosystèmes terrestres les plus riches en espèces et parmi les moins bien connus (Gentry 1992). La caractérisation et la compréhension des facteurs qui régissent la diversité tropicale a inspiré des générations d'écologues, permettant des avancées fondamentales en écologie théorique et évolutionniste (Chazdon & Whitmore 2002). Pourtant, ces études se sont concentrées sur les vertébrés et les plantes, négligeant la plupart des taxons d'invertébrés, malgré qu'ils représentent la majorité de la diversité en eucaryotes dans ces milieux (May 2011). Les forêts tropicales sont notamment les milieux les plus riches en arthropodes terrestres (Miller *et al.* 2002) avec 1,5 million d'espèces décrites et plus de 10 millions d'espèces estimées (Hamilton *et al.* 2010). Et parmi les arthropodes tropicaux, les araignées sont un des taxons les plus diversifiés avec au moins plusieurs centaines d'espèces par hectare de forêt et une diversité estimée à au moins un millier d'espèces par forêt (Agnarsson *et al.* 2013). Pourtant, nous en savons toujours peu sur la diversité en espèces des assemblages d'araignées tropicales aux échelles locale (entre habitats) et régionale, et en conséquence sur les facteurs qui déterminent cette diversité. Ce manque de connaissance est lié à l'extrême diversité des milieux tropicaux, qui complexifie l'étude des patterns et processus à son origine.

Les difficultés de l'étude de la diversité des araignées tropicales

Caractériser et comprendre les assemblages hyperdiversifiés comme ceux des araignées tropicales est une tâche écrasante mais nécessaire. D'autant plus nécessaire dans le contexte actuel de réchauffement climatique et de perte d'habitats due à la déforestation qui frappe durement les écosystèmes tropicaux (Malhi *et al.* 2008), qui voient leur diversité disparaître avant même d'avoir pu être décrite. Les arachnologues tentent de décrire cette diversité depuis plus de trente ans (e.g. Coddington *et al.*, 1991) et accumulent les difficultés méthodologiques liées à l'extrême diversité des assemblages et au manque de connaissances à leur sujet (Coddington *et al.* 2009).

Les résultats des études menées ces dernières années sur la standardisation des méthodes d'échantillonnages (Sørensen *et al.* 2002, Coddington *et al.* 2009, Malumbres-Olarte *et al.* 2017) et des méthodes d'analyse (Chao & Jost 2012, Chao, Gotelli, *et al.* 2014) permettent de produire un ensemble de recommandations pour l'étude des assemblages hyperdiversifiés.

Repenser l'échantillonnage pour le milieu tropical

L'échantillonnage en milieu tropical nécessite **de repenser les stratégies et méthodes d'échantillonnage utilisées du fait de l'extrême diversité en espèces des assemblages.**

Acquérir des données précises et comparables sur des assemblages hyperdiversifiés nécessite d'appliquer des **protocoles d'échantillonnage fiables, efficaces et standardisés**.

- (i) Malheureusement, les protocoles qui suivent de tels critères restent rares et il n'est pas certain qu'ils puissent être appliqués aux communautés hyperdiversifiées d'arthropodes des milieux tropicaux (Malumbres-Olarte *et al.* 2017). Il est donc nécessaire de **développer des protocoles standardisés spécialement adaptés aux milieux tropicaux**.
- (ii) D'autre part, les études s'étant attelées à tester la pertinence des protocoles et méthodes couramment utilisées sur les assemblages d'espèces d'araignées à travers le monde ont mis en évidence que mêmes les échantillonnages intensifs en milieux tropicaux sont biaisés négativement par le sous-échantillonnage (Novotný & Basset 2000, Sørensen *et al.* 2002, Coddington *et al.* 2009, Agnarsson *et al.* 2013), lequel se traduit par une forte propension d'espèces singletons (représentées par un seul individu), et cause une sous-estimation de la richesse réelle des assemblages. Aussi, **l'intensité d'échantillonnage** nécessaire pour avoir une idée fiable de la richesse en espèce en milieu tropical est largement supérieur à celle connue en milieu tempéré.
- (iii) Enfin, le gradient vertical connu de la végétation tempérée n'est pas retrouvé en tropical (Basset *et al.* 2003) et la stratification de l'arthropofaune dans la végétation ne semble pas suivre les mêmes lois qu'en tempéré (Basset *et al.* 1992, 2003). Les **méthodes d'échantillonnage** utilisées sont donc susceptibles de ne pas avoir la même efficacité. Il est donc nécessaire de questionner et tester la pertinence de ces méthodes dans le cadre de l'échantillonnage des assemblages hyperdiversifiés des forêts tropicales.

Prendre en compte le sous-échantillonnage

Les **méthodes statistiques** utilisées pour déterminer les patterns et facteurs à l'origine de la diversité des assemblages hyperdiversifiés doivent **prendre en compte leur sous-échantillonnage**. Étant donné que plus on échantillonne d'individus, plus on trouve d'espèces (Gotelli & Colwell 2001), et d'espèces rares, il est possible que la richesse des échantillons ne se stabilise pas lorsque la taille de l'échantillon augmente, dans un schéma d'échantillonnage réaliste (Coddington *et al.* 2009, Chao, Gotelli, *et al.* 2014). Il est donc nécessaire d'utiliser des **estimateurs de diversité** tenant compte de la **complétude** (ou couverture) de l'échantillonnage (Jost 2010, Chao & Jost 2012), c'est-à-dire de la proportion des espèces ayant été échantillonnée.

Travailler avec des espèces inconnues

Enfin, la troisième difficulté rendant complexe l'obtention de données précises et comparables sur les assemblages d'espèces d'araignées tropicales repose sur le fait que ces araignées ne sont pas connues.

De manière générale, les araignées sont un taxon pour lesquels l'identification à l'espèce est complexe et nécessite les connaissances taxonomiques d'experts. Or le nombre d'experts est trop faible pour décrire toutes les espèces. Dans le cadre des assemblages tropicaux d'araignées, la majorité des espèces ne sont donc pas décrites (Robinson *et al.* 2009, Cardoso, Pekár, *et al.* 2011) et les assemblages sont extrêmement diversifiés (Agnarsson *et al.* 2013). Coddington *et al.* (2009) estime que la diversité en araignées en forêts tropicales humides non perturbés est rarement inférieur à plusieurs centaines d'espèces par hectares. Or les ressources en taxonomistes ne sont pas suffisantes pour délimiter et décrire les espèces en même temps que l'on étudier les assemblages (Agnarsson *et al.* 2013). Il est donc nécessaire de recourir à des approches de para-taxonomie en identifiant les individus à la morpho-espèce (Oliver & Beattie 1993, 1996b, a) : on identifie des taxa, séparables sur la base de différences morphologiques évidentes, sans connaissances a priori. Dans certains cas cependant, e.g. les araignées loups (Lycosidae), l'approche à la morpho-espèce n'est pas suffisante car le conservatisme morphologique est tel qu'il nous manque des caractères informatifs pour définir et séparer les espèces et même les genres (Vink *et al.* 2002). En conséquence, leur diversité ne peut être étudiée que par des approches moléculaires.

Les araignées tropicales étant relativement peu décrites, la seule possibilité pour étudier leur diversité en trait est de les mesurer (Schuldt *et al.* 2014, Liu *et al.* 2015, Schuldt & Staab 2015, Pétillon *et al.* 2018). La classification des guildes de chasse à elle été adaptée aux araignées des milieux néotropicaux (Höfer & Brescovit 2001, Dias *et al.* 2009). Celle-ci met en évidence que l'on trouve, chez les araignées néotropicales, une variation de guildes de chasses au sein d'une même famille d'araignées entre les genres (**Encadré 5**), e.g. on trouve chez les Lycosidae des araignées chasseuses à vue, des araignées qui tissent des toiles et d'autres sédentaires qui creusent des terriers. De plus, les connaissances sur l'histoire naturelle et l'écologie des araignées néotropicales sont si lacunaires qu'il sera nécessaire de revoir cette classification à mesure de l'accumulation des connaissances sur ces araignées (Höfer & Brescovit 2001, Dias *et al.* 2009).

La majeure partie des araignées tropicales n'ayant pas été décrites par la science, chaque nouvel échantillonnage contient nécessairement des espèces observées pour la première fois (Agnarsson *et al.* 2013). Aussi, il est nécessaire de s'intéresser à étudier les phylogénies de ces araignées afin de pouvoir décrire leurs patterns de diversité et les intégrer aux études à l'échelle des assemblages.

À notre connaissance, il n'existe pas à ce jour d'étude qui s'intéresse aux trois composantes de la diversité (taxons, traits et unités évolutives) sur les assemblages d'araignées en milieu tropical.

OBJECTIFS ET ORGANISATION DE LA THÈSE

Cette thèse s'inscrit dans le cadre général de la description des patterns de diversité et de la caractérisation des processus écologiques qui les déterminent à l'échelle des assemblages. Ce questionnement est ancien en écologie mais n'a pas trouvé de réponse globale car les patterns de diversité et les processus à leur origine varient entre groupes d'organismes et, pour un même groupe, entre écosystèmes. Les araignées, car elles sont un groupe abondant et diversifié avec une forte importance écologique sont un groupe modèle en écologie dont l'étude devrait permettre de mieux comprendre les processus responsables des patterns de diversité. Leurs patterns de diversité semblent être déterminés principalement par des processus écologiques déterministes liés à leur environnement s'appliquant à des échelles locales. Les milieux tropicaux, de par leur très grande diversité en araignées et en habitats, sont des milieux qui permettent de tester les processus écologiques à l'origine des patterns de diversité. À ce jour, ces avancées sont toutefois grandement limitées par l'absence quasi-totale de connaissances sur la diversité des araignées dans ces écosystèmes.

Dans ce contexte, la problématique de cette thèse est la suivante : **quels sont les patterns de diversité et les processus qui en sont responsables chez les araignées dans les milieux tropicaux ?**

L'originalité de cette thèse est notamment d'utiliser des approches taxonomiques (**Partie I et II**), traits (**Partie II**) et phylogénétiques (**Partie III**) pour décrire les patterns de diversité des araignées à des échelles principalement locales dans différents habitats tropicaux.

Caractériser les patterns de diversité des araignées tropicales passe par le développement de protocoles d'échantillonnage fiables et la comparaison des méthodes d'échantillonnage (**Chapitre 1 et 2**). Les connaissances sur la taxonomie et les traits des araignées étant lacunaires, il est nécessaire d'avoir recours à des approches de para-taxonomie (**Chapitre 1, 2, 3 et 4**), des approches phylogénétiques (**Chapitre 5**) ainsi que de tester différents traits (**Chapitre 4**) afin de décrire les patterns de diversité. La réalisation d'études comparatives des patterns de diversité dans différents habitats (**Chapitre 1, 2, 4 et 5**) et entre biomes (**Chapitre 3**) permet alors de faire des hypothèses sur les facteurs structurant la diversité. Dans l'ensemble, ces approches complémentaires donnent un aperçu plus complet des patterns de diversité des araignées des milieux tropicaux..

Dans la **Partie I** de cette thèse nous nous sommes intéressés à la détermination de la diversité en taxons d'assemblages d'araignées de différents habitats néotropicaux ainsi qu'à l'étude des facteurs la structurant en appliquant des protocoles standardisés, testant les méthodes d'échantillonnage, utilisant l'approche morpho-espèce et en standardisant les analyses statistiques en utilisant des estimateurs de richesse.

- Dans le **premier chapitre** (Privet *et al.* 2020), nous nous sommes concentrés sur les assemblages d'araignées de la strate du sol, en comparant l'efficacité de

deux méthodes d'échantillonnage couramment utilisées pour cette strate pour décrire les patterns de diversité des assemblages d'araignées le long du gradient de complexité d'habitats.

- Dans le **second chapitre** (Privet *et al.* 2018), nous avons développés et testés un protocole d'échantillonnage quasi-optimal (i.e., optimisé pour plusieurs sites) pour caractériser la diversité des araignées du sol et de la végétation et étudier les variations de diversité des assemblages entre deux types d'habitat tropicaux forestiers.

Dans la **Partie II** de cette thèse nous avons exploré l'apport de la prise en compte de la diversité en trait pour décrire et comprendre les patterns de diversité des assemblages d'araignées dans différents habitats néo-tropicaux.

- Dans le **troisième chapitre** (Privet & Pétilion 2020), nous avons comparé les patterns de diversités taxonomique et en traits entre écosystèmes tropicaux et tempérés.
- Dans le **quatrième chapitre** (Privet *et al.* en préparation), nous avons testés différents traits et comparé les diversités taxonomique et en traits afin de déduire les facteurs qui déterminent les assemblages.

Dans la **Partie III**, nous avons utilisé l'outil phylogénétique pour déterminer les patterns de diversité d'une famille d'araignées dans un archipel tropical aux conditions écologiques très diversifiées et mettre en évidence le rôle des différents habitats dans la radiation évolutive de celle-ci.

- Dans le **cinquième chapitre** (Privet *al.* en préparation), nous avons déterminé les patterns de relations phylogénétiques entre les araignées vivant des différents habitats et fait des inférences sur l'origine de leur radiation.

Dans la **Discussion générale**, nous discutons de l'ensemble de ces résultats et ouvrons des perspectives de recherche sur les patterns et processus de diversité des araignées tropicales.

En annexe sont présentés les travaux auxquels j'ai participé en parallèle de cette thèse. L'**Annexe 1** (Lowe, [...], Privet *et al.* 2020) encourage la création d'une base de données mondiale ouverte sur les traits des araignées et pose les bases de celle-ci. L'**Annexe 2** (Pekàr, [...], Privet, *et al.* 2021) présente la base de trait mondiale des araignées (World Spider Trait Database). L'**Annexe 3** (Courtial, Privet, Picard & Pétilion, submitted) présente une description d'espèce d'araignées sauteuses (Salticidae) de forêt tropicale par une approche de taxonomie intégrative. L'**Annexe 4** (Pétilion, Privet, *et al.*, 2020) présente une étude portant sur les assemblages d'araignées dans les fragments de forêts Hawaïen et l'occurrence croissante des espèces exogènes dans ces assemblages.

PARTIE I : FACTEURS STRUCTURANT LA DIVERSITÉ TAXONOMIQUE DES ARAIGNÉES TROPICALES

STANDARDISATION MÉTHODOLOGIQUE ET ÉVALUATION DES FACTEURS ÉCOLOGIQUES INFLUENÇANT LA DIVERSITÉ TAXONOMIQUE DES ARAIGNÉES ENTRE HABITATS TROPICAUX

Comment étudier les facteurs structurant la diversité taxonomique des assemblages d'araignées dans les habitats tropicaux ?

CHAPITRE.1

Efficacité relative des pièges barbers par rapport à la chasse à vue de nuit dans l'évaluation de la diversité des araignées du sol le long d'un gradient structurel d'habitat néotropicaux

Relative Efficiency of Pitfall Trapping vs. Nocturnal Hand Collecting in Assessing Soil-Dwelling Spider Diversity along A Structural Gradient of Neotropical Habitats

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Abstract

Assessing spider diversity remains a great challenge, especially in tropical habitats where dozens of species can locally co-occur. Pitfall trapping is one of the most widely used techniques to collect spiders, but it suffers from several biases, and its accuracy likely varies with habitat complexity. In this study, we compared the efficiency of passive pitfall trapping versus active nocturnal hand collecting (NHC) to capture low understory-dwelling spider taxonomical (morphospecies) and functional (hunting guilds) diversity along a structural gradient of habitats in French Guiana. We focused on four habitats describing a structural gradient: garden to the orchard to the forest edge to the undisturbed forest. Overall, estimated morpho-species richness and composition did not vary consistently between habitats, but abundances of ground-hunting spiders decreased significantly with increasing habitat complexity. We found habitat-dependence differences in taxonomic diversity between sampling strategies: NHC revealed higher diversity in the orchard, whereas pitfalls resulted in higher diversity in the forest. Species turnover resulted in high dissimilarity in species composition between habitats using either method. This study shows how pitfall trapping is influenced by habitat structure, rendering this sampling method incomplete for complex, tropical environments. However, pitfall traps remain a valuable component of inventories because they sample distinct assemblage of spiders.

Key-words: Araneae; Guiana shield; sampling methods; diversity indices; functional diversity; species richness; turnover.

Introduction

Spiders constitute a mega-diverse taxon, with more than 48,000 species described to date [1] and still many new species found every year. To get reliable estimates of local spider diversity, ecologists and conservationists need a robust sampling protocol, i.e., standardized (repeatable in space and time, without introducing bias), and optimized (with a maximized ratio of sampling effort by collected diversity) for realistic sampling given time and resource constraints [2–4]. To achieve such a standardized and optimized sampling protocol, the selection of cost-effective complementary methods is a critical issue [5]. Previous work on sampling protocol optimization was mainly conducted in Mediterranean and temperate systems (see [3,4]), but few studies have compared methods in highly diverse systems such as tropical forests [6,7]. Yet, it remains unclear which sampling protocol would provide reliable estimates of spider diversity in tropical systems. Because spiders have developed a wide range of hunting strategies (e.g., ambushing, wandering, web building, door trapping) and inhabit varied habitats and vegetation strata (from the ground to canopy), several sampling methods need to be integrated to get a reliable description of the whole assemblage. Nevertheless, the number of collecting methods should be limited to minimize the complexity of a sampling protocol and to maximize its repeatability. The objective of this study is, therefore, to evaluate the robustness of sampling methods in tropical forests. In that respect, we focused on tropical low understory-dwelling spiders because there is less consensus to sample this stratum in forests despite its lower spider diversity compared to other strata [6,7].

Previous studies on low understory-dwelling spiders showed that this stratum needs to be studied with special care in order to obtain representative estimates [8–10], especially because sampled diversity changes with the sampling method [11,12]. In tropical forests, however, there is no consistency between the methods used to sample low understory-dwelling spiders. For example, Vedel et al. [13] used hand collection and litter sifting, Malumbres-Olarte et al. [6] used hand collection, cryptic searching, and pitfall traps, and Privet et al. [7] used pitfall traps and litter sifting.

Pitfall trapping is the most widely used arthropod sampling technique to collect spiders worldwide [12,14–16]. This method was shown to be efficient in catching ground-dwelling spiders in a variety of ecosystems, including temperate forests [17], Mediterranean shrublands [3], agrosystems, and grasslands [11,18], and bare grounds [19]. However, pitfall traps appear to be less efficient in tropical forests [6,7,13], and they may suffer from several important biases, including the under-studied effect of habitat structure [20,21].

Together with litter sifting (specially designed for small and low mobile species: [7]), nocturnal hand collecting (NHC) is an alternative method to sample low understory-dwelling spiders. This method was found to be efficient by Azevedo et al. [5], in particular, as it shows no bias between day and night spider diversity sampling in tropical forests [7,22]. Yet, depending on the collectors' experience, NHC is cheap and requires less effort than pitfall traps [5,23].

Hence, it is still unclear whether pitfall trapping should be used to perform a standardized protocol, or whether nocturnal hand collecting should be included to develop an optimized protocol. Moreover, although the efficiency of pitfall trap sampling is likely to be influenced by habitat structure, as with other passive methods, no study to date has assessed how its efficiency could change along a structural gradient of habitat.

Here we compare the efficiency of two widely used sampling techniques, pitfall traps, and NHC, to capture **taxonomic** and **functional diversity** of low understory-dwelling spider assemblages along a broad gradient of tropical habitats in French Guiana. We hypothesize that the sampling efficiency of passive methods (i.e., pitfall traps) would decrease when habitat structural complexity increases [20]. In contrast, we predict little variation in sampling efficiency for the active method of NHC [21].

More precisely, we expect a difference in the estimated taxonomic diversity between methods to increase along the increasing gradient of habitat structural complexity (tested by comparing rarefaction curves between methods habitat by habitat). Second, we expect species composition of spider assemblages to differ between methods and vary more with habitat structure with pitfall traps than with NHC (tested by determining beta diversity between methods per habitat and beta diversity between habitats per method). Finally, we hypothesize that hunting guilds diversity (a proxy of the functional diversity assessed by guilds composition and relative abundances per method per habitat) would be more affected by changes in habitat structural complexity with pitfall traps than with NHC.





Materials and methods

Site

To compare the efficiency of low understory-dwelling spider sampling methods along a structural gradient of Neotropical habitats, we focused on four different land-use types along the road Degrad Saramaka, near Kourou, in French Guiana. The habitats sampled were: (i) home garden, (ii) small orchard after slash and burn, (iii) forest edge, and (iv) undisturbed tropical forest (see Table 1 for GPS [global positioning system] coordinates, pictures, and Corine Land Cover codes). The garden habitat had the least vegetation cover with mainly short cut grass, some herbaceous patches, a few ornamental flower bushes (*Ixora* sp. [species]), and some young trees such as mango trees. The orchard habitat was a lowland rain forest cut out and planted with tree species producing fruits (mango, banana, lemon, orange, cashew nut, coconut, and other palm trees), a variety of bushes (pineapple, spinach, and manioc) and some herbaceous cover. The forest edge was adjacent to a road and an open area such as gardens. It was 50 meters deep into the vegetation, so its aspect was similar to forest areas. The forest was a primary lowland tropical rain forest area with the typical vegetation of seasonally flooded forest of coastal French Guiana. We established one plot of 50m x 50m in each of the four land-use types, and inside an area of 20 km² (Table 1) to limit changes in soil type and hydrological characteristics. The local climate is typically equatorial with a fairly constant

temperature across the year (around 26.1 °C with 1.3 °C difference between the lowest and the highest temperature for 2001–2012) with high humidity divided into two main seasons: heavy rainfall between December and August and dry with few rains between September and November, giving an average annual precipitation about 283 cm per year [24].

Table 1. Coordinates and Corine Land Cover Classes of the four habitats along the habitat complexity gradient.

				
	Garden	Orchard	Edge	Forest
GPS coordinates	5°04'43.3"N 52°40'36.8"W	5°04'58.6"N 52°41'47.3"W	5°04'15.0"N 52°41'33.8"W	5°04'11.4"N 52°41'48.1"W
Corine Land Cover 2012 code and libellee	2430 – Land principally occupied by agriculture, with significant areas of natural vegetation	3111 – Broad-leaved forest	3111 – Broad-leaved forest	3111 – Broad-leaved forest

Sampling protocol

In order to sample ground-dwelling spiders, we used circular pitfall traps and NHC. Following the COBRA protocol [4,15], we set up 25 pitfall traps (eight centimeters in diameter) in a grid of 5 m × 5 m in each plot (five lines of five pitfalls spaced by 10 m across each 250 m² plot). The pitfall traps were filled one-third full by ethylene glycol for killing and preserving specimens fallen in the traps. The pitfall traps remained active 15 days. In each plot, this method required a team of two people working two hours to install 25 pitfall traps and one hour to collect samples, resulting in a total effort of six person-hours per plot. While the pitfall traps were active, we sampled spiders using NHC along the lines traced by pitfalls. This method required two experienced persons sampling low understory with a headlamp for half an hour during night-time in each plot looking for moving spiders and eyeshine. This gave a sampling effort of one person-hour per plot for NHC. Sampling was conducted from the 15th to the 29th of July 2013, corresponding to the end of the raining season in French Guiana. The climate in July 2013 in Kourou oscillated between 28 to 33 °C, with an average of 4.46 mm of precipitation per day [25].

Taxonomy

Individuals were sorted and identified at the species level, defining morpho-species when there were no matching species in the literature [13,26–28]. Spider samples, separated by morpho-species from each sampling technique, were stored in 70% ethanol. When juvenile spiders were old and characteristic enough to be identified at the species level, we included them. All spiders are deposited within the reference collections of the UMR EcoFoG, Kourou (French Guiana).

Hunting guilds

Trait functions have not been explicitly tested for spiders, especially in tropical habitats, and using traits when there is no evidence for their functionality runs the risk of attributing patterns in community functional structure to false mechanisms [29]. Here we assessed functional diversity by assigning hunting guilds to genera and families. We are aware that guilds describe more a group of species than a functional attribute per se [30] and that guild classification at the family or genus level does not integrate inter- nor intraspecific variability [31], which are important in structuring assemblages. We followed the hunting guilds classification described in Cardoso et al. [31], except for Trechaleidae placed in specialists by Cardoso et al. [31] and described as hunters by Dias et al. [32]. The guilds were the following: (1) sensing, (2) sheet, (3) space, (4) orb-web weavers; (5) specialists; (6) ambush, (7) ground, and (8) other hunters.

Data analysis

The 25 pitfall traps per habitat were pooled to make pitfall samples comparable to one hour NHC per habitat (following [6] methods and results). Taxonomic diversity per sampling method was assessed using rarefaction and extrapolation curves based on sample coverage [33,34]. We characterized the taxonomic alpha diversity of spider communities using complementary species and abundance-based indices: (i) taxonomic richness, (ii) Shannon, and (iii) Simpson diversities [33]. Analyses were completed using the R-based iNEXT package [33,35]. Extrapolations were realized using the asymptotic Chao1 estimator [36]. 95% confidence intervals (CI) were calculated, and non-overlapping of CI indicates a difference at a level of 5 percent between expected diversities [33]. Changes in species composition (taxonomic beta diversity) (i) between methods within a habitat and (ii) between habitats per method were assessed by computing pair-wise dissimilarities on abundance data using the Bray indices family and separating the turnover and nestedness-resultant components of taxonomic beta diversity using the betapart R package [37,38]. Guilds composition and relative abundances were compared between methods and habitats (i.e., pitfall garden vs. NHC garden; pitfall orchard vs. NHC orchard, etc.). Changes in guild composition were tested by statistically comparing the relative abundance of the dominant guilds among habitats using χ^2 tests. All analyses were conducted using the R software version 3.4.3 [39].

Results

We sampled a total of 355 spiders (213 adults and 142 juveniles) representing 18 families and 40 morpho-species (see Table S1 for composition). Similar total numbers of individuals were collected by both methods, 174 by pitfall traps and 181 by NHC.

Among the 18 morpho-species that were not singletons, four (22%) were collected by both methods. The NHC technique collected specimens belonging to 28 morpho-species from 11 families and representing seven hunting guilds (ground, other and ambush hunters, sheet, orb, sensing web weavers and specialists). Pitfall traps sampled spiders from 18 morpho-

species from 11 families representing four hunting guilds (ground hunters, other hunters, sensing web weavers, and specialists).

Patterns of taxonomic alpha diversity were consistent between diversity metrics (i.e., species richness, Shannon and Simpson indices); taxonomic alpha diversity was significantly higher in the orchard but lower in the forest when using hand-collection compared to a pitfall, and it showed no differences between the methods in the garden and edge (Figure 1). Yet, taxonomic alpha diversity did not consistently vary with habitat complexity.

Species composition collected by the two methods was almost completely dissimilar. This dissimilarity was mainly due to species turnover in all habitats, except in gardens where assemblage composition was much more similar between methods. In this case, the few differences were linked to assemblage nestedness (Table 2). Assemblages were almost

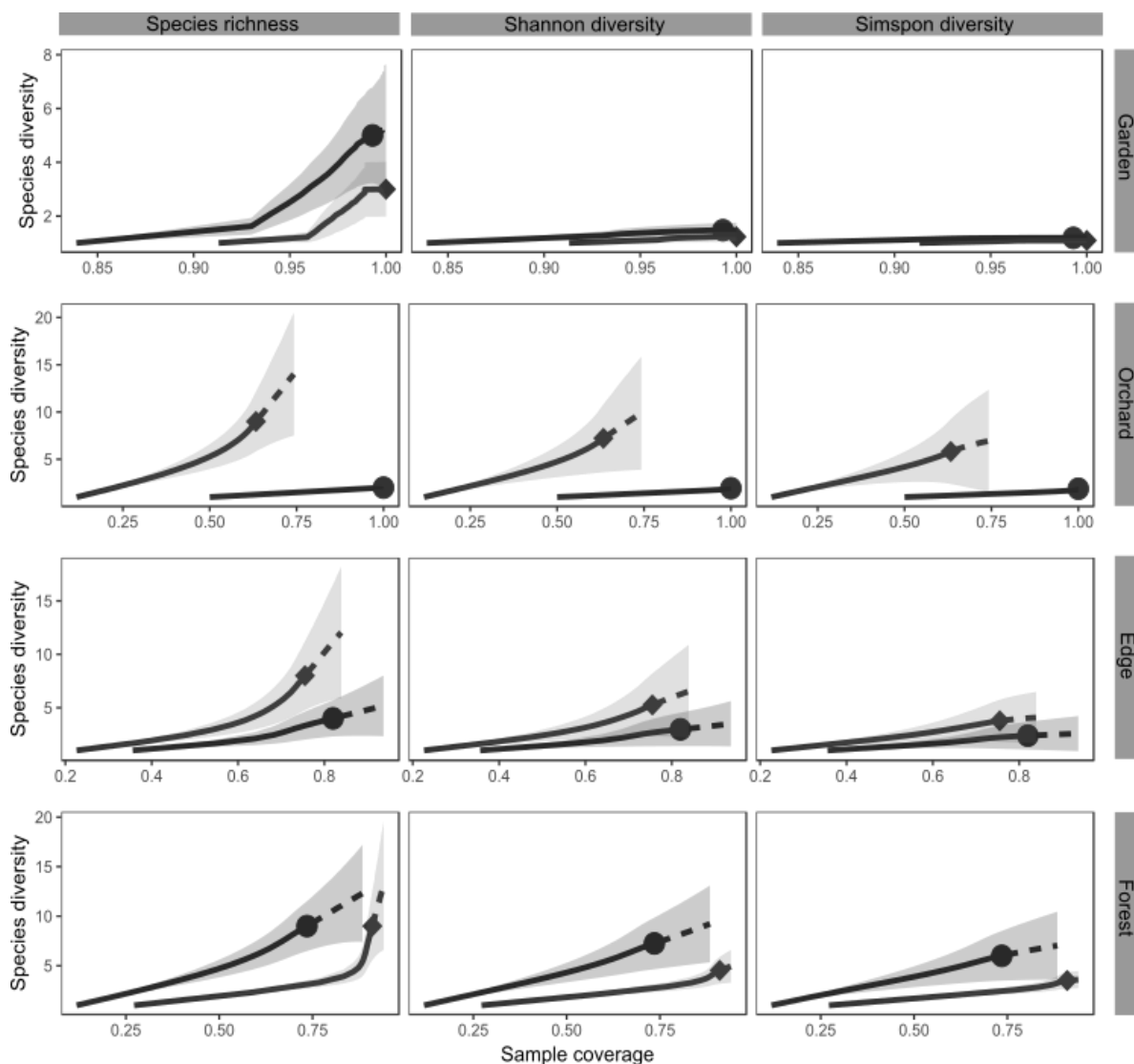


Figure 1: Estimated taxonomic diversity (species richness, Shannon and Simpson diversities) in all 4 habitats for each sampling method. 95% confidence intervals are represented in light color and were obtained by 200 bootstrap replications. Plain lines represent interpolated diversity whereas dotted lines extrapolated.

completely dissimilar among habitats for both methods, and this dissimilarity was mostly due to species turnover (Table 3).

Table 2. Species composition dissimilarity and its decomposition by habitat between pitfall traps vs. nocturnal hand collecting (β : beta diversity = total dissimilarity between pitfall and NHC; β_{TURN} : partition of the beta diversity linked to turnover; β_{NEST} : partition of the beta diversity linked to nestedness).

	Garden	Orchard	Edge	Forest
β	0.22	1	0.93	0.81
β_{TURN}	0.05	1	0.9	0.61
β_{NEST}	0.17	0	0.03	0.20

Table 3. Decomposition of beta diversity among habitats and by sampling methods (β : beta diversity; β_{TURN} : partition of the beta diversity linked to turnover; β_{NEST} : partition of the beta diversity linked to nestedness).

	Garden			Orchard			Edge		
<i>Pitfall</i>	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}
Orchard	1	1	0						
Edge	0.97	0.8	0.17	1	1	0			
Forest	1	1	0	1	1	0	0.93	0.9	0.3
<i>NHC</i>	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}	β	β_{TURN}	β_{NEST}
Orchard	0.9	0.68	0.22						
Edge	1	1	0	1	1	0			
Forest	1	1	0	1	1	0	0.89	0.8	0.09

Guild composition significantly changed among habitats for both methods when considering pitfall traps and NHC separately (χ^2 tests, 6df, $\chi^2 = 403.97$, and $\chi^2 = 274.29$, $p < 0.001$, respectively) with a replacement of ground hunters by other hunters and web builders. On the other hand, patterns of guild relative abundance differed between methods only for the orchard and forests (Figure 2).

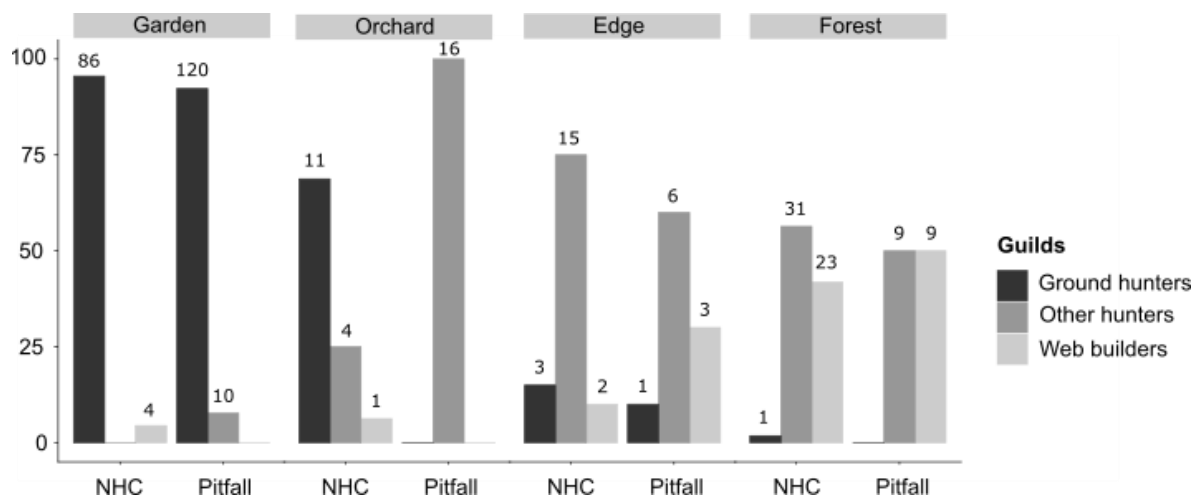


Figure 2: Relative abundance in hunting guilds along the structural gradient of habitats collected by Nocturnal Hand Collecting (NHC) and pitfall traps. For simplification purpose, we grouped guilds as follows: (1) ground hunters: ‘ground hunters’, (2) other hunters regroups the ‘other hunters’, ‘ambush hunters’ and ‘specialists’ guilds, and (3) web builders: ‘sensing web weavers’, ‘sheet web weavers’, ‘space web weavers and ‘orb web weavers’. Absolute numbers are presented above each bar.

Discussion

In this study, we compared for the first time the efficiency of the two most common sampling methods to collect tropical soil-dwelling spiders, namely pitfall traps and Nocturnal Hand Collecting (NHC), across contrasting habitats in French Guiana. Our results showed that the difference between the two methods in capturing soil-dwelling spider taxonomical diversity varies according to the sampled habitat, though not consistently. Although we performed intensive sampling, the number of individuals was low, and the proportion of singletons was high, which is typical of tropical forests where many species are locally rare [40].

Differences in taxonomic alpha diversity between pitfall trapping and NHC did not significantly increase along the structural gradient of habitats. Contrary to our expectation that the difference of estimated taxonomic diversity between passive and active methods increases along the increasing gradient of habitat structural complexity, we actually found that taxonomic alpha diversities differed between methods only in orchard and forest. Our results in garden and forest edge are in line with two previous studies performed in the Mediterranean and temperate ecosystems [5,15] that found pitfall traps and NHC to be both efficient methods to collect soil-dwelling spiders.

However, NHC was more efficient than pitfall traps to collect spider taxonomic alpha diversity in orchard, what may be due to the fact that pitfall traps would capture only species that actively hunt, while NHC would allow sampling species with a wider variety of hunting strategies (such as traps, silk nets or ambushing). Indeed, this was confirmed by our finding

that NHC captures a more functional diversity of spiders than pitfall traps in this habitat. This result is in line with those of Sereda et al. [41], who found that hand-collection was better than pitfall traps for capturing ground-dwelling spider diversity in a temperate forest. Conversely, NHC was less efficient than pitfall traps to collect spider taxonomic richness in tropical rainforests. NHC efficiency relies on the sight of the person who samples, which would be reduced by the complexity and heterogeneity of the tropical rainforest habitat. The experience of collectors can also play an important role, which was not the case here because all collectors were experienced. Previous studies found that pitfall traps were unsuitable in estimating the diversity of ground-dwelling predators like spiders in tropical rainforests and other temperate woody habitats [5–7,20,42]. Here we showed that neither pitfall traps nor NHC alone are sufficient for sampling the whole taxonomic alpha diversity of ground-dwelling spiders in Neotropical forests. Even if we choose to compare one-hour NHC (2 people, ½ hour per person) with the pool of 25 pitfall traps left 15 days on the field (versus five pitfall traps left for 5–8 days in [6]), we still observed that pitfall traps and NHC result in a similar number of sampled individuals. Comparing taxonomic alpha diversity relatively to sample completeness, our results suggest that an increase in sampling effort with NHC will not allow its efficiency to surpass those of pitfall traps. Further methodological investigations comparing other sampling methods such as litter sifting [7] or hand collection in quadrats [23] are thus needed to get proper estimation of the diversity of ground-dwelling spiders in tropical rainforests.

In addition, the taxonomic composition of spider assemblages was almost completely different when sampled by pitfall traps and NHC, and this dissimilarity was linked to species turnover except in the garden habitat. Contrary to our expectation, the difference in taxonomic composition between methods did not increase along the increasing gradient of structural habitat complexity. Moreover, taxonomic beta diversity was not more affected by changes in habitat complexity with pitfall traps. As NHC and pitfall traps do not sample the same species, both methods should be used concomitantly when aiming at inventorying spiders in tropical habitats. The fact that turnover of spider assemblages was driven by species turnover rather than by nestedness has already been reported from a large variety of habitats, such as temperate wet meadows, ponds and grasslands [43–45], forests [46], grey dunes [47] or African mountains [48]. In the garden habitat, assemblages sampled by NHC and pitfall traps were less dissimilar, and this dissimilarity was mostly linked to species nestedness: there were species and abundance loss between the methods, and no species replacement. Gardens are less complex, more open, and disturbed than other habitats. Its spider assemblage is very little diversified, as exemplified by the strong dominance of one single species (a Lycosidae). Consequently, pitfall traps and NHC sample nearly the same spider assemblage in this highly disturbed habitat, and may be interchangeable when sampling Neotropical garden, and other habitats with simple structure and low relative diversity. On the other hand, one should also consider that the small number of morpho-species common to both methods could be the result of the high proportion of singletons. As singleton proportion can be reduced by

increasing sampling effort (although most tropical species are considered few abundant), the composition distinctiveness of these two methods could also decrease.

One intriguing aspect of our results concerns the proportion of male and female caught during the sampling. Pitfall traps are known to catch mature males to a higher degree than other sampling methods, including NHC, due to higher reproductive activity of males. Consequently, pitfall traps catch a larger percentage of identifiable spiders. If we confirm that pitfall traps caught more adult spiders, we, however, found that both methods catch more females than males. Considering spider functional beta diversity (assessed by hunting guilds), dissimilarities between methods did not increase along the increasing gradient of habitat complexity, contrary to our prediction. NHC sampled higher guild richness in all habitats, which suggests that NHC is more efficient than pitfall trapping for collecting the overall functional diversity of soil-dwelling spiders in Neotropical habitats. However, both NHC and pitfall traps showed the same gradual change of guild composition across habitats, with a shift from ground hunters dominated-assemblages in garden habitat to assemblage dominated by 'other hunters' in forests (i.e., other hunters and ambush hunters, sensu [31]). Hence, even if pitfall traps collect fewer guilds, they still capture important elements of functional diversity. These results are in line with those found along an urban-rural transect in temperate regions [49], although functional changes were not systematically reported [50,51].

Unlike studies performed on other biomes, we suggest an optimized protocol using NHC to collect soil-dwelling spiders rather than pitfall traps in relatively simple tropical habitats (i.e., gardens, orchards, and edges) for ecological studies because it collects higher taxonomic and guild diversity and requires up to six-fold lesser sampling effort than pitfall traps, while still capturing similar abundances of soil-dwelling spiders and guilds shift along gradient. However, following Tourinho et al. [52], we suggest that NHC alone is not sufficient to provide a complete picture of spider assemblages in tropical habitats and should be used in association with beating tray methods. Besides, we showed that the efficiency of NHC is more limited than pitfall traps in complex habitats such as neotropical forests, which contradicts previous results (e.g., [6]). Knowing that pitfall traps are less efficient than litter sifting in the tropical forest [7], we suggest to combine NHC with litter sifting as based-methods for ecological studies of ground-dwelling spiders in this habitat, complemented by beating methods as well. However, we recommend studies with inventory purposes to use a combination of these methods as NHC and pitfall traps sample different species assemblages.

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<i>Pisauridae</i> sp.1									1
<i>Thaumasia</i> sp.13									22
Salticidae									
<i>Salticidae</i> sp.39	2								
Segestriidae									
<i>Segestriidae</i> sp.1		1							
Sicariidae									
<i>Sicariidae</i> sp.1									1
Sparassidae									
<i>Sparassidae</i> sp.7									1
Tetragnathidae									
<i>Leucage</i> sp.2									1
Trechaleidae									
<i>Trechalea</i> sp.1									1
<i>Trechalea</i> sp.8									1
<i>Trechaleidae</i> sp.9									1
<i>Trechaleidae</i> sp.6									1
TOTAL	130	90	16	16	10	20	18	55	

CHAPITRE.2

Structure des assemblages d'araignées dans un complexe forêt humide-inselberg néotropical : aperçu écologique et méthodologique d'une étude intensive à petite échelle

Spider assemblage structure in a neotropical rainforest-inselberg complex: ecological and methodological insights from a small-scale intensive survey

Kaïna Privet, Cyril Courtial, Thibaud Decaëns, El Aziz Djoudi, Vincent Vedel, Frederic Ysnel & Julien Pétilion
Tropical Ecology (2018) **59**(1): 21-34.

[**Erratum**]: during the writing of this thesis we detected some missing sentences to the published version of this article that we added.

Abstract

Despite the huge diversity tropical arthropods represent, factors shaping their communities are still poorly known, especially at small spatial scales. In this study, we aimed at providing ecological and methodological insights from a short and intensive field sampling of spiders, a highly diverse group of predators. We investigated how sampling methods, habitat type and day-time affect diversity and composition of spider assemblages. The standardized sampling protocol was applied in a tropical rainforest in French Guiana, where both ground- and vegetation-dwelling (up to 2.5 meters) assemblages were sampled during day and night using supposedly complementary methods at low and high (granitic hills called inselbergs) elevations. Observed and estimated richness of vegetation-dwelling spiders, as well as their species composition, did not differ between methods (sweep netting vs. beating). Observed species richness was much lower in pitfall traps than in litter samples, which suggests a low mobility of ground-dwelling spiders and reveals the inadequacy of the former method compared to the latter. Spider assemblage in the vegetation of inselberg was two times poorer than in lowland forests and dominated by different families, probably due to harsher habitat conditions there. Strongly different patterns were here highlighted between vegetation and ground-dwelling spider assemblages, the latter being less diversified than in the vegetation which deserves further attention.

Key words: Araneae, composition, day-time, French Guiana, non-parametric estimators, richness, sampling method.

Introduction

Assessing spatial patterns in organisms' diversity, and understanding their ecological determinants, is still one of the most fundamental topics in modern ecology. Yet our knowledge derives primarily of vertebrates and plants studies; much less is known about the structure of terrestrial arthropod communities despite they represent the most diversified taxa with highest species richness. Arthropods are especially speciose in tropical rainforests where nearly 1.5 million species have been currently described out of an estimated number of 3 to 11 million tropical rainforests could host (Hamilton *et al.* 2010, 2013).

Among terrestrial arthropods, spiders are one of the most diversified group of arthropod predators worldwide (Nentwig 2013), with high bio-indicative values (e.g. Marc *et al.* 1999). Indeed, spiders are abundant occupying a wide range of spatial niches (Kremen *et al.* 1993) and inhabit almost every terrestrial habitat. Numerous studies have investigated the driving factors of spider assemblages in temperate habitats, such as vegetation structure, or habitat management (e.g. Hatley & Macmahon 1980; Lafage *et al.* 2015; Prieto-Benitez & Mendez 2011; Scharff *et al.* 2003). However, we still know much less regarding the factors that drive spider assemblages in tropical forests, where most of the studies have been carried out with inventory objectives or at the population level (Azevedo *et al.* 2014; Coddington *et al.* 1991; Dias *et al.* 2009; Scharff *et al.* 2003; Sereda *et al.* 2014; Sørensen *et al.* 2002). This is particularly true in French Guiana where spider assemblages have been the subject of several inventory surveys (see Vedel & Lalagüe, 2013; Vedel *et al.* 2015) and where a list of spiders have been recently updated (Vedel *et al.* 2013) but where the determinants of assemblages are still misunderstood. Tropical rainforests of the Guiana Shield are characterised by the existence of different and contrasting forest habitats. They differ in their ground texture and fertility, their seasonal water stress and the associated forest structure (Baraloto *et al.* 2011). These habitats included "terra firme" to seasonally flooded lowland rainforest and sometimes rocky outcrops named inselbergs, which rise abruptly from the surrounding landscape. Lowland rain-forests lie in low-lying areas near rivers where episodic flooding often submerges ground surfaces during periods of high precipitation (Baraloto *et al.* 2007). At the opposite, inselbergs exhibit very particular ground and microclimate conditions: alternation of heavy rain and severe drought with air temperature and insolation that regularly reach values that are considerably higher than average values in surrounding forests (Kounda-Kiki *et al.* 2004). Then, inselbergs are considered as "xeric island" or "microclimatic desert" (Porembski 2007). Vegetation of inselbergs is starting to be known, and studies highlighted that these habitats host a characteristic vegetation mosaic (Porembski 2007; Sarthou *et al.* 2003, 2010). In contrast, little research has been devoted to the fauna of inselbergs ecosystems, especially for invertebrates (Kounda-Kiki *et al.* 2004; Lees *et al.* 2014; Sarthou *et al.* 2009; Vedel & Lalagüe 2013) and spiders (Vedel *et al.* 2013). Inselbergs are considered less rich than surrounding rainforest, but to date no direct study have compared their assemblage to that of other forest habitats.

Even in well studied tropical habitats, spider assemblages, as for arthropods in general, are larger than measured due to high frequencies of rare species (in average 32% of singletons;

Coddington et al. 2009) whatever the sampling effort. Tropical forest sampling of spider is then a difficult task with the need of using a combination of different sampling methods (e.g. Cardoso et al. 2009; Jiménez-Valverde & Lobo 2005) and a high sampling effort to collect a significant part of the fauna (Coddington et al. 2009). Thus, it has been underlined that to get significant knowledge on the ecology of particular indicator taxa, quasi-optimal design (sensus Malumbres-Olarte et al. 2017) using complementary sampling methods is still needed. Moreover, comparisons based on observed species numbers are misleading and could have important implications in answering ecological questions. In addition, day vs. night period sampling seems to be an important factor influencing the composition of spider assemblages (Cardoso et al. 2009; Coddington et al. 1991; Sørensen et al. 2002) and could potentially explain part of singletons due to nocturnality (Coddington et al. 2009). In fact, spiders are known to be mostly active only at night and a smaller proportion is active only during the day (Foelix 2010).

In this study, we applied an intensive quasi-optimal protocol by day and night on vegetation- and ground-dwelling spider assemblages from inselberg and lowland rainforests at the Nouragues National Nature Reserve in French Guiana. We focused on species richness and assemblage composition as the main response variables (e.g. Azevedo et al. 2014; Coddington et al. 1996; Lafage & Pétilion 2016; Prieto-Benitez & Mendez 2011) with the aim of investigating the effect of habitat type on diversity and composition of spider assemblages

We focused on spider assemblages of the two more accessible strata: understory vegetation and ground leaf litter. In understory stratum, the two sampling methods known to be the most efficient are the sweep net and beating tray. These methods target different microhabitats with sweep net targeting lower understory vegetation and the beating tray higher understory vegetation (Coddington et al. 1991; Vedel & Lalagüe 2013). Regarding the ground stratum, pitfall traps remains one of the most widely used methods for studying ground-dwelling macro-arthropods in general (Spence & Niemelä 1994) and especially spiders, while depletion quadrat with litter sifting, despite being time-consuming, also seems to represent an interesting complementary method (e.g. Baars 1979; Mantzouki et al. 2012). As we used two different and supposedly complementary methods on each stratum, during two periods of the day, we also aim at bringing some new method-logical insights on spider sampling in tropical rain forests, particularly in inselberg forests.

More specifically, we tested the following hypotheses. (i) Microhabitat influence the diversity of vegetation-dwelling spider assemblages. We thus expect species richness and composition to be different between both sampling methods targeting understory vegetation. Moreover, these two sampling methods sampled different volumes of habitat (i.e. sweeping sampled twice the volume of habitat of beating). Thus, we expected spider species richness to follow changes in the volume of habitat sampled by the different methods. (ii) Pitfall trap sampling can be considered as a surrogate of other, time-consuming, sampling methods like litter sifting (e.g. Baars 1979; Mantzouki et al. 2012) for ground-dwelling spiders. Thus we expected species richness, abundances (caught by pitfall traps) and densities (caught

by litter sifting) to be correlated, whereas composition was expected to differ slightly between methods, with more mobile species caught by pitfall traps. (iii) Diversity of spider assemblage changes along with the type of tropical forest habitat. We expected vegetation and ground-dwelling spider assemblages' species richness to be less rich in inselberg forests compared to lowland forest due to harsh climate conditions and less depth of ground layer found on inselbergs (Kounda-Kiki et al. 2004). In the same way, we expected the species composition of spider assemblages to be significantly different between inselberg and the nearby lowland forests, as it has been found for vegetation (Porembski 2007; Sarthou et al. 2010). (iv) Daytime influences the activity of vegetation and ground-dwelling spiders. Thus, night assemblages were expected to be richer than day ones (Foelix 2010) and to have different species composition (Cardoso et al. 2011).

Materials and methods

Study site

The fieldwork was carried out in the Nouragues national nature reserve (French Guiana; 4°04'18"N; 52°43'57"W). Sampling was done during nine consecutive days and nights early during the rainy season (6–15 December 2013), which is considered by Vedel & Lalagüe (2013) as the best sampling period. It was achieved in two rainforest habitats: (i) lowland seasonally flooded rainforest located in the Pararé area, and (ii) low forest located on the top of the Nouragues inselberg (411 m above sea level). Lowland vegetation is typical of primary lowland rainforest, with few inclusions of different vegetation types: palmito-swamp forests, liana forests and bamboo forests. Canopy height varies between 30 and 50 m. The Nouragues inselberg is a rocky outcrop isolated from the rest of the forest where the ground is washed away and the ground granitic. Hence, only a few but specialized species survive in this harsh environment (Porembski 2007). The low forest found nearby the top of this inselberg is rich in Myrtaceae with many endemic plants. It is characterized by a significant number of shrubby species or small bushy shrub with multiple stems and trees with leaning stems. Other trees have tapering trunk. Canopy height ranges from 8 to 15 m high.

Sampling design and field work

A standardized protocol was established to assess differences between lowland and inselberg habitats on spider rainforest assemblages inhabiting the ground and understorey vegetation, and to compare assemblages observed during day vs. night collecting for both strata. This protocol is described, tested and criticized for the first time in this study.

Two surface-standardized active sampling methods targeting understorey vegetation species were selected. First, sweep netting was carried out in the lower herb layer or shrubby vegetation with a sweep net along 20 m long and one meter wide (arm length plus sweep handle) transects, representing a sampling volume of 50 m³ each. Twelve stratified transects were conducted per period (day and night) by the same two persons.

The second method consisted in vegetation beating to collect spiders living in the shrub, high herb vegetation, bushes, and small trees. A stout stick was used to hit branches or other vegetation in order to collect falling specimen on a beating tray placed underneath. These samples were conducted in 9 × 9 m quadrats where the vegetation was beat to a height of 2.5 m allowing to sample about 22.5 m³. Twelve stratified quadrats were conducted per period (day and night) by two duos concurrently (six quadrats per duo).

As in our protocol, sweep netting sampled twice the volume-habitat of beating, we investigate if species richness of assemblage collected followed the same pattern, i.e. being two times richer by sweep netting than by beating.

Two methods were used to sample ground-dwelling assemblages. First, pitfall traps constituted by circular, 10 cm diameters, plastic traps containing ethylene glycol as a preservative were used. Fifteen pitfalls have been arranged along a line, spaced 10 m apart (Topping & Sunderland 1992), and were set over a period of two days (days plus nights) in each habitat. They allow to estimate the abundance of ground-dwelling spiders. The second method consisted in litter sifting conducted by using a Winkler extractor as a depletion method to estimate the density of spiders on 1 m² as in Groc et al. (2009), hereinafter called 'litter sifting'. Hand sorting of this samples were conducted in lab. Fifteen 1 m² litter samples were spatially pair-matched with pitfall traps and conducted per day and per night (total thirty). Pitfall traps and litter samples were spatially paired to test if pitfall traps can be considered as surrogate of litter sifting.

A total of 186 samples were collected from the Nouragues Nature Reserve, 96 from vegetation and 90 from ground, with 93 samples from each habitat (see Table 1).

Table 1. Summary of spider sampling by each method, for both lowland and inselberg habitats. Nb.: number, ad.: adults, prop.: proportions.

	Inselberg				Lowland				Total
	Pitfall	Litter	Beat	Sweep	Pitfall	Litter	Beat	Sweep	
Nb. replicates	15	30	24	24	15	30	24	24	-
Nb. Individuals (ad.)	35 (21)	51 (15)	196 (66)	205 (64)	23 (4)	77 (20)	270 (101)	404 (109)	1261 (420)
Nb. morphospecies	12	14	44	38	4	17	66	80	216
Prop. singletons (%)	67	93	80	71	100	82	74	71	67
Prop. doubletons (%)	25	0	9	8	0	18	11	15	18

Sorting and identification

Samples were fixed and preserved in 70% ethanol. Individuals were first sorted and identified to family following Dippenaar-Schoeman & Jocqué (1997), Adis (2002), and Jocqué & Dippenaar-Schoeman (2006). Because of the lack of taxonomical knowledge about tropical spiders we defined morpho-species (MS) based on morphological traits, mainly by observation of genitalia and habitus. Under a 65 microscope, we realized a side-by-side comparison of specimens to determine distinct morphological entities. Both juveniles and adults were identified at the family level. Because only adults are identifiable at species level, no morpho-

species was defined based on juveniles. Juveniles were then excluded of the richness measures, although they represented ~60% of the specimens. When it was possible, sexes were matched based on color patterns and physical characteristics. For each identified morpho-species a unique code was assigned and a reference individual was designated to take images of dorsal and ventral body views and genitalia. All individuals are deposited at the University of Rennes 1 (Rennes, France).

Statistical analyses

Correlation between pitfall traps and litter sifting

To test if pitfall sampling can be considered a surrogate of litter sifting, we used correlation to compare pair-matched data using $\log(x+1)$ transformed data. Litter sifting, and especially pitfall trap, collected few adult spiders (Table 1). There was no significant difference between abundances (pitfall traps) and densities (litter sifting) (Generalized Linear Model, abundances ~ methods, $F_{1,0.2} = 1.57$, $P = 0.21$) and there were either not significantly correlated (Spearman correlation test, $r = -0.17$, $P = 0.38$, $n = 30$). Hence data from pitfall traps were omitted from subsequent analyses.

Influence of methods, habitat, daytime and strata on morphospecies richness

To test if habitat, daytime, methods and strata influence observed species richness, generalized linear models (GLM) were carried out. First, a model comprising all factors and their interaction was carried out. Type of error (Poisson vs. Quasi-Poisson) was selected by comparing residual deviance and denominator freedom degree (O'Hara & Kotze 2010). A second model was calculated if interaction was not significant. We estimated the expected species richness by using different non-parametric estimators: Abundance-based Coverage Estimator (ACE) (Chao & Yang 1993), Incidence-based Coverage Estimator (ICE) (Lee & Chao 1994), Chao1 and Chao2 (Chao 1984 1987), Jackknife 1 and Jackknife 2 (Burnham & Overton 1978, 1979), which determined the least number of species present in the assemblage (Mao & Colwell 2005). Such estimators do not show dependence to unequal sampling effort between modality (Basset et al. 2012) and they show little dependence to number of rare species, however a minimum sampling effort is needed to produce a reliable estimation (Chao et al. 2009). Richness estimators were compared using species rarefaction curves (Gotelli & Colwell 2001). Sample coverage was calculated for each sample according to Chao & Jost (2012) method and sampling intensity was calculated as the ratio of adult number on species richness (Coddington et al. 1996).

Influence of methods, habitat and daytime on assemblage composition (morpho-species)

To test for differences in assemblage composition between methods (beating vs. sweeping and pitfall vs. sifting), habitat (inselberg vs. lowland forest) and daytime (day vs. night samples), we conducted an analysis of similarities using PERMANOVA (PERmutational

Multivariate ANalysis Of VAriance, 9999 permutations) on the corrected Bray-Curtis index (Clarke et al. 2006).

Analyses were made using R software (R Development Core Team 2013), except richness estimators that were calculated with EstimateS software (Colwell 2013).

Results

A total of 1261 spiders were collected belonging to 35 families and 216 morpho-species. Among them, 1075 vegetation-dwelling spiders (17% adults) and 186 ground-dwelling spiders (32% adults) were collected with a high proportion of singletons (67%; Table 1). The intensity of this sampling was 1.9.

Influence of methods, habitat and daytime on species richness

Despite the difference in sampled habitat volume between both vegetation sampling methods, sampling intensity was nearly the same with 1.5 and 1.7 for beating and sweeping on the inselberg and 1.5 and 1.6 in lowland, respectively. Observed richness was not significantly different between methods used to sample vegetation-dwelling spiders (Table 2). Non-parametric richness estimators did not highlight high differences between beating and sweeping methods (Table 3). Estimators never stabilized with the increase of number of individuals sampled as neither of species rarefaction curves reached an asymptote (Fig. 1).

Observed species richness was significantly higher in lowland than in inselberg for vegetation-dwelling spiders (Table 1; Fig. 2), but not for ground-dwelling spiders collected by litter sifting where there was no difference of observed species richness between both habitats (Table 2). The different non-parametric richness estimators comparing habitats did not show an asymptote with the increase of sample set (Fig. 3). These curves showed that the expected richness was higher in lowland than in inselberg for both ground and vegetation assemblages. Moreover, the sample coverages were very small for all samples with 46% of the estimated fauna diversity sampled by beating, 58% by sweeping, 63% by pitfall trap and 14% by litter sifting on the inselberg, and 52%, 55%, 0% and 32%, respectively, in lowland rainforest. Comparisons of the estimated species richness (Table 3) show that the estimated species richness is higher in lowland compared to inselberg forests for vegetation-dwelling spiders, but it is higher in inselberg forests for ground-dwelling spiders.

There was no significant difference in species richness between day and night for both vegetation and ground-dwelling spider assemblages (Table 2).

The sampling intensity was nearly the same for both strata with an average of 1.12 for the ground and 1.54 for the vegetation. Vegetation-dwelling species richness was significantly higher than that of ground (Generalized Linear Model, richness \sim strata, $F_{1,36} = 160.76$, $P < 2.2e^{-16}$; Table 1), which was confirmed by the rarefaction curves showing that estimated species richness was higher for vegetation-dwelling spiders than ground-dwelling ones.

Table 2. Effects of methodological and ecological factors on spider species richness (GLM).

Strata tested	Variable tested	Source of variation	F	df	P
Vegetation	Richness	Model 1 (test for interaction)			
		Method	0.7	1	0.391
		Habitat	30.7	1	3.079e⁻⁷
		Period	0.7	1	0.391
		Method x habitat	2.1	1	0.152
		Method x period	0.7	1	0.394
		Habitat x period	0.2	1	0.650
		Method x habitat x period	0.2	1	0.652
		Model 2 (no interaction)			
		Method	0.7	1	0.389
Ground (litter)	Richness	Model 1 (test for interaction)			
		Habitat	0.3	1	0.613
		Period	0.3	1	0.613
		Habitat x period	0.2	1	0.641
		Model 2 (no interaction)			
Habitat	0.3	1	0.61		
Period	0.3	1	0.61		
Ground vs. vegetation	Richness	Model 1 (no interaction)			
		Strata	160.8	1	<2.2e⁻¹⁶

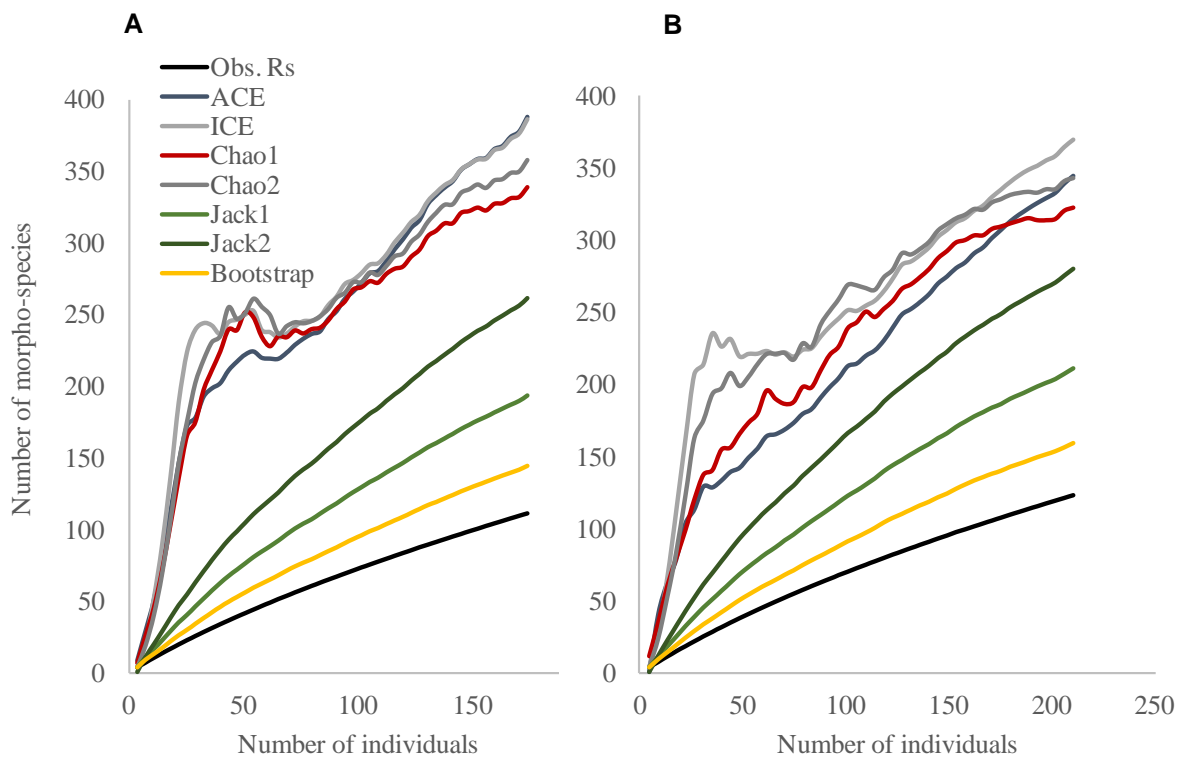


Fig. 1: Comparison of species rarefaction curves between beating (A) and sweep netting (B) obtained with seven non-parametric estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2 and Bootstrap). Obs. Sr: observed species richness.

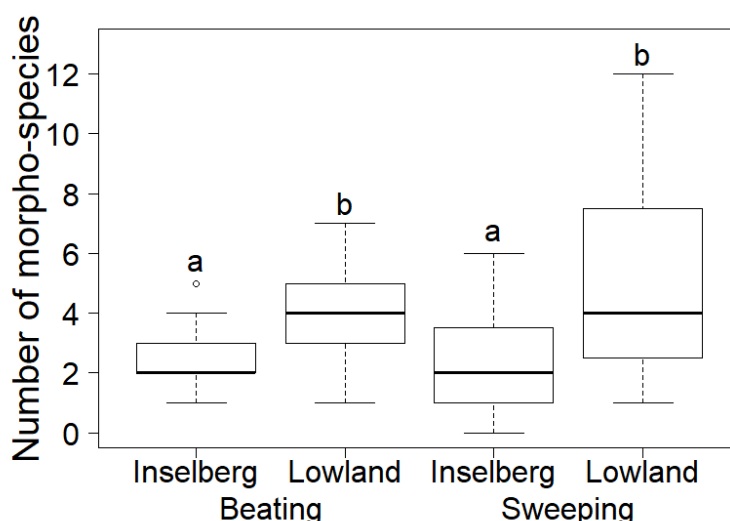


Fig. 2: Comparison of mean observed species richness between lowland and inselberg habitats, for each vegetation sampling method

Table 3: Observed and estimated species richness for the four sampling methods in both habitats. Obs.: observed.

		Obs.	Chao1	Chao2	Jack1	Jack2	ACE	ICE	Bootstrap
Inselberg	Beat	44	190	186	84	115	184	169	62
	Sweep	38	146	121	73	98	103	126	54
	Pitfall	12	22	22	19	23	35	33	15
	Litter	14	50	52	27	38	105	107	19
Lowland	Beat	66	269	303	122	166	223	239	91
	Sweep	80	252	257	150	199	230	244	113
	Pitfall	4	9	10	8	11	9	10	5
	Litter	17	39	51	32	44	57	81	23

Influence of methods, habitat, daytime and strata on composition

Difference in morpho-species composition between sweeping and beating was non-significant (PERMANOVA, $R^2 = 0.01$, $P = 0.51$).

Significant difference in morpho-species composition was found between inselberg and lowland vegetation-dwelling assemblages (PERMANOVA, $R^2 = 3.14$, $P = 1e^{-4}$). There were 176 morpho-species identified in vegetation samples (Table S1). Among them, only 19 were shared by inselberg and lowland assemblages (*i.e.* 11%), 51 were specific to inselberg (*i.e.* 29%) and 106 to lowland (*i.e.* 60%). Morpho-species belonging to the families Mimetidae and Uloboridae were only found on the inselberg while those belonging to Ctenidae and Linyphiidae were found only in lowland (Fig. 4). But the main morpho-species difference between both habitats was primarily due to four of the richest families: Theridiidae, Salticidae, Thomisidae and Araneidae. In fact, 78% of Theridiidae were specific to lowland, 11% shared to both habitats and 11% specific to inselberg. As well as 63% of Salticidae were specific to lowland, 13% common and 25% specific to inselberg; and respectively 60%, 29%, 13% of Thomisidae and 57%, 12%, 31% of Araneidae. On the contrary, there was no significant

difference in morpho-species composition of ground-dwelling samples (PERMANOVA, $R^2 = 0.045$, $P = 0.21$), but only one morpho-species was common to lowland and inselberg litter ground samples (Table S2).

There was no significant difference between day and night morpho-species abundances (*i.e.* composition) between day and night for vegetation-dwelling (PERMANOVA, $R^2 = 0.01$, $P = 0.52$) and ground-dwelling assemblages (PERMANOVA, $R^2 = 0.05$, $P = 0.11$).

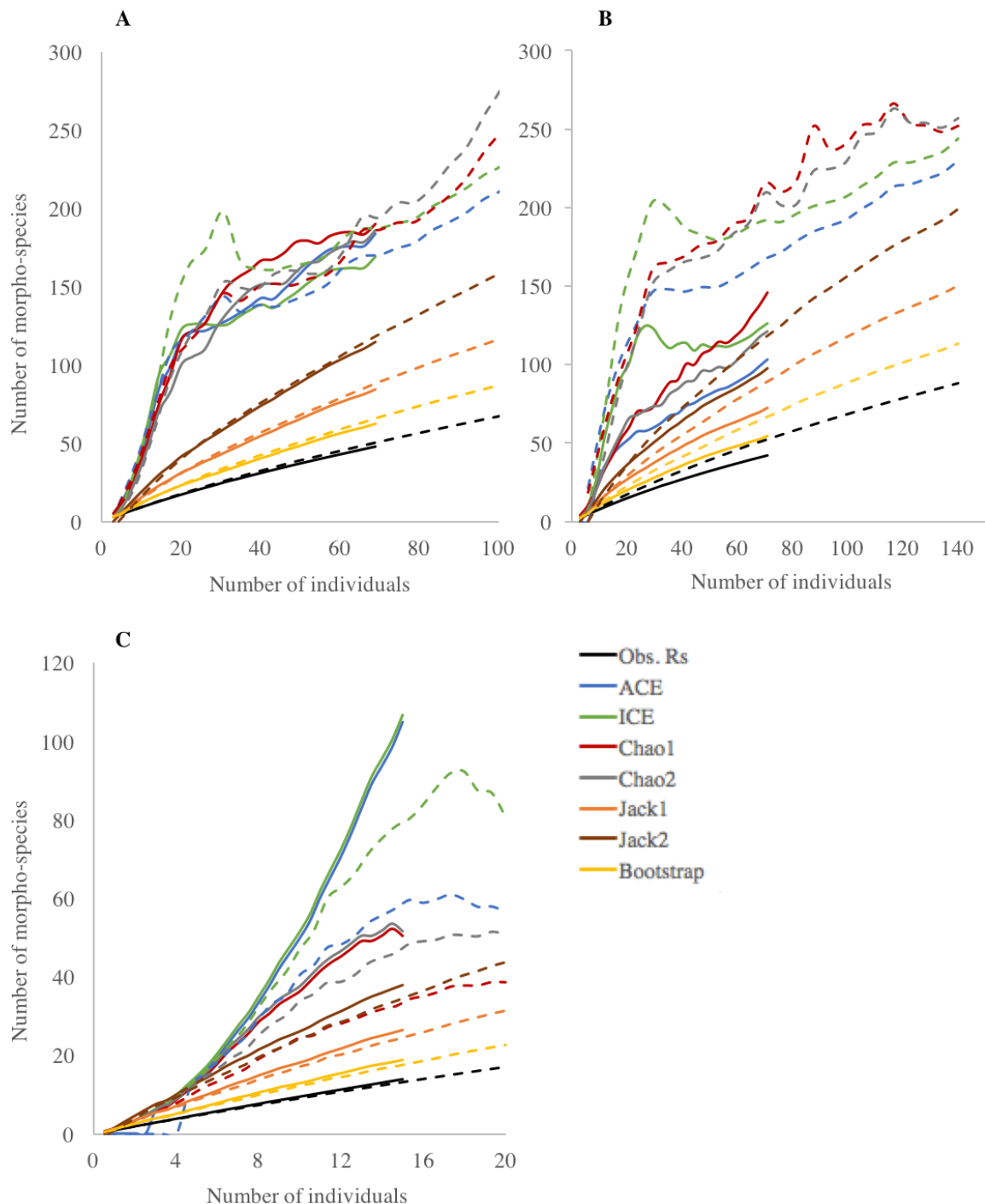


Fig. 3: Comparison of species rarefaction curves between inselberg (solid line) and lowland (dotted line) habitats obtained with seven non-parametric estimators (ACE, ICE, Chao1, Chao2, Jackknife 1, Jackknife 2 and Bootstrap) for 3 different sampling methods: sweep netting (A), beating (B) and litter sifting (C).

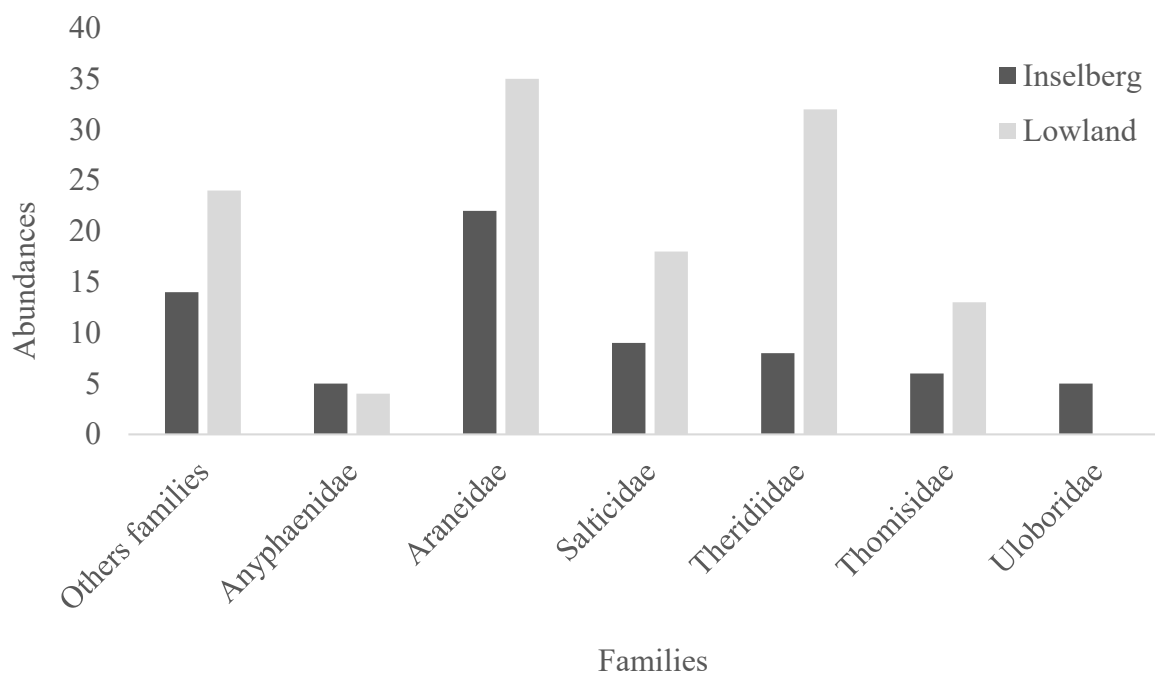


Fig. 4: Comparison of abundances by spider family between inselberg and lowland forest (vegetation samples only).

Discussion

The present study is the first application of a quasi-optimised protocol developed to answer ecological questions about tropical arthropod assemblage, particularly to compare unknown inselberg's assemblage to the little better described lowland's. Thanks to an intensive field survey, we can bring both ecological and methodological insights by using a highly diversified group, spiders, as a model. Despite a high sampling effort, the sampling intensity is still low and the proportion of singletons is high (*sensu* Coddington et al. 2009). This typically shows the difficulty to reach exhaustive inventory, which was not our objective, when targeting mega-diverse taxa like spiders.

Comparison of sampling efficiency between methods

When doubling the volume of habitat sampled (here two times higher by sweeping than by beating), the observed species richness of vegetation-dwelling spiders did not significantly increase. Sweeping allowed to collect more individuals, but not more species. Instead, a doubled habitat volume did not increase the sampling efficiency. That is invalidating our first hypothesis: species richness does not linearly increase with the volume of habitat sampled. According to Rosenzweig (1995), species richness can logarithmically increase with sampling area. Hence, it would probably be necessary to increase the volume of habitat sampled more than expected to get a significant increase in species richness. Moreover, none of the species rarefaction curves reached an asymptote, which shows that the sampling effort was not

sufficient for both methods to collect a representative part of the spider fauna. In addition to the low abundance of most of the morpho-species collected, this suggests that the scale at which sedentary tropical arthropods should be sampled is frequently underestimated (Chao et al. 2009; Coddington et al. 2009), probably due to aggregate patterns of fauna in tropical forests. On the other hand, this absence of significant difference between sweeping and beating species richness could also be related to the fact that these methods sampled different subsets of spider assemblages, i.e. lower understory vegetation for sweep netting and higher for beating (Cardoso et al. 2008; Scharff et al. 2003; Vedel & Lalagüe 2013). However, we found no difference of composition between these two sampling methods.

Pitfall traps collected only few ground-dwelling spiders while litter sifting collected much more. We found no correlation between species richness by pitfall traps and spatially paired litter sifting samples and no correlation between number of individuals by both methods, i.e. abundances (pitfall traps) and densities (litter sifting). Thus, pitfall sampling cannot be considered as a surrogate of litter sifting. Pitfall traps seems to be not suitable to estimate abundance and diversity of ground-dwelling predators like spiders in tropical rainforests, which conforms few previous studies on spiders (Azevedo et al. 2014; Luff 1975; Maelfait & Baert 1975; Malumbres-Olarte et al. 2017) and on neotropical harvestmen (Tourinho et al. 2014). Three alternative explanations can be proposed to explain this result. (i) Pitfall traps samples collected less spiders because they do not capture cursorial spiders. But then densities by litter sampling would have been even higher: thus, this explanation is considered unlikely. (ii) Another explanation is that pitfall traps are less efficient than active ground sifting method because ground-dwelling spiders have a low mobility. This has been suggested in temperate forests by Siewers et al. (2014) for small, web-building species. (iii) It has been previously suggested that systematic and standardized designs may not adequately reflect the abundance and composition of spider assemblages because of environmental gradients and microhabitats (e.g. presence or absence of herb layer) that are not correctly encompassed by pitfall sampling (Cardoso et al. 2009; Sereda et al. 2014). Our results showed that pitfall traps do not allow to collect high number of spiders in tropical habitats, and we thus consider this method as unsuitable for such tropical habitats (to the difference of temperate, arctic and Mediterranean habitats where it is more effective and commonly used: see e.g. Cardoso et al. 2008; Scharff et al. 2003). This lack of efficiency should be considered to standardize further samplings of tropical ground-dwelling spiders.

Comparison of spider assemblages between inselberg and lowland forests

Inselberg forests are isolated on a rocky outcrop, characterized by harsh microclimatic conditions, poor and shallow ground, and the vegetation found there is poorer than that of surrounding, lowland, rainforests (Porembski 2007). Although the importance of inselberg forest biodiversity has been shown for vertebrates and plants (e.g. Fredericksen et al. 2003; Girão et al. 2010; Porembski 2007), we found only three studies

that investigated the difference of arthropod richness and composition between lowland tropical rainforest and low forests located on the top of adjacent inselbergs (canopy spiders: Russell-Smith & Stork 1994; ground-dwelling Scarabaeidae: Feer, 2013; ground and understory spiders: Vedel & Lalagüe 2013). In their study, Vedel & Lalagüe (2013) compared abundance, richness and diversity of spiders between one inselberg forest plot and three lowland forest plots. They found greater species richness in lowland forests spiders than in the low inselberg forest, which was explained by the differences in local habitat conditions (mainly higher moisture in lowland forests) between habitats. Feer (2013) observed the same pattern regarding the ground-dwelling Scarabaeidae. However, Vedel & Lalagüe's work was a pilot study with methodological and inventory objectives undertaken with non-optimal conditions (i.e. low sampling effort, sampling during periods of low abundance for arthropods), with no spatial replication and the authors did not perform statistical tests on their data. In some Indomalayan rainforests, Russell-Smith & Stork (1994) found an increase in canopy spider abundance and richness with increasing altitude. Yet the fact that the spiders they studied were located in another biome and in the canopy make their results hard to compare to ours.

The present study partially confirmed Vedel & Lalagüe (2013) results, and supplemented them in terms of assemblage composition, also indicating contrasted results between strata. As a matter of fact, observed and estimated species richness of vegetation-dwelling spiders were higher in lowland forests than on the top of inselberg inselberg but an opposite pattern was found for ground-dwelling spiders estimated species richness using litter sampling. Litter depth has generally direct and positive effects on spider assemblages (Uetz 1979), as well as for the ground-dwelling arthropods of tropical lowland rainforests (Ashford et al. 2013). This is overall consistent with a bottom-up control of spider density and diversity (e.g. Bennett 2010). However, we found that ground-dwelling spiders were not poorer on inselberg where the ground is shallow. We assumed three alternative and non-exclusive explanations for this pattern: (i) ground hygrometry and periodic flooding could be a more limiting for the ground-dwelling spiders of lowland forests than the harsh climatic conditions and shallow ground on the Inselberg and (ii) flooding in lowland forest is a factor of litter homogenization (Adis & Junk 2002; Decaëns et al. 2016; Lafage & Pétilon 2016), which could result in decreased spider abundance and richness there. Moreover, (iii) inselberg are considered as functional islands (Prance et al. 1996; Sarthou et al. 2017) and low forests growing are more seen as ecotone (Sarthou et al. 2010) that would generate rainforest biodiversity thanks to environmental heterogeneity (Smith et al. 1997). While the species composition was studied in Vedel & Lalagüe (2013) only in lowland tropical rainforests, our study gives for the first time knowledge about spider assemblage composition on an inselberg, and its comparison to the spider composition of an adjacent lowland forest provided. The change in morpho-species composition observed in vegetation-dwelling spiders supports the idea that inselbergs act as a habitat very distinct from the surrounding forests. These tropical forest habitats host different spider assemblages, with for example less Theridiidae than in lowland suggesting that the vegetation structure complexity is lower in this habitat (Hatley & Macmahon 1980).

However, morpho-species occur in low numbers. Accordingly, further studies are needed to investigate a gradual shift in composition from lowland to the top of inselbergs. Furthermore, no difference of observed diversity nor composition between habitats was found for ground-dwelling spiders, probably because the number of individuals were too low. Nonetheless, another study conducted at the same place on ground-active Ctenids found differences in spider densities between elevations using hand-collections in depletion quadrats (Pétillon et al. 2018).

Influence of day-time collecting

Several tropical studies revealed a higher spider richness at night (Coddington et al. 1991; Green 1999; Sørensen et al. 2002) and change in species composition between day and night (in tropical: Malumbres-Olarte et al. 2017; Sørensen et al. 2002; temperate: Cardoso et al. 2008). It has consequently been argued that spiders should be sampled both day and night in temperate and tropical forests (see Cardoso et al. 2009 and Vedel & Lalagüe 2013, respectively).

Conforming few other studies, our results showed no difference in spider species richness (see Coddington et al. 1996; Dobyys 1997 and Vedel et al. 2015 for temperate and tropical forests, respectively) and composition (see Cardoso et al. 2008 & Sørensen et al. 2002; Malumbres-Olarte et al. 2017 for temperate and tropical forests, respectively) between sampling times. Vedel et al. (2015) suggested that collecting spiders at only one time during the day was enough to estimate the diversity of spider assemblages across vegetation types. However, the lack of consensus emerging from the different studies on species composition implies that it is necessary to collect spiders during both day and night to confirm that period has no significant influence on the composition. Further-more, sampling during both periods is still necessary to describe and inventory the diversity of spider assemblages (Malumbres-Olarte et al. 2017).

Due to the poor abundances collected by pitfall traps, comparison during both periods has only been conducted on assemblage collected by litter sifting. Ground-dwelling assemblages were then not significantly different between sampling periods. Litter sifting can only catch spiders when they are out of their refuge. Unlike what is usually reported on spider species inhabiting the leaf litter (Vedel et al. 2015), our results showed that these spiders are not more active (i.e. foraging) at night.

However, we cannot rule out the possibility that the absence of difference can be due to the low numbers of individuals collected here and generally in tropical samples because it probably had a direct influence on the assemblage composition.

Comparison of spider assemblages between ground and vegetation strata

Estimated species richness was much lower at ground surface compared to the surrounding vegetation (data from the same sampling stations by beating and sweep-netting). Such a difference between ground and vegetation strata is surprising because their diversities

are likely correlated in arthropods (Donoso et al. 2010, but see Mathieu et al. 2009 with low spider densities in an Amazonian grassland). Moreover, ecological comparisons of ground- and vegetation-dwelling spider assemblage conducted in this study highlighted that ground and vegetation patterns in species richness are different. Vegetation-dwelling spider richness was indeed lower on the inselberg compared to the lowland forest and composition changed between both habitats, whereas observed species richness and composition did not change between habitats for ground-dwelling and estimated species richness was higher in inselbergs. These results suggest that species diversity is probably not correlated between ground- and vegetation-dwelling spiders. Considering that the number of species living together reflects the richness of adaptive opportunities, species richness is the result of inter-specific competition and factors that conditioned productivity, as well as niche size, quantity of resources (Ricklefs 1979). Hence, lowered abundances and species richness of ground-dwelling spiders would reflect a high competition with other predators such as ants, one of the most diverse taxa on tropical ground and low available resources due to a high rate of recycling (due to ants or environmental conditions) (Ashford et al. 2013; Malumbre-Olarte et al. 2017). Accordingly, ground and vegetation samples are not redundant and both are essential to fully understand the influence of ecological factors in shaping spider assemblages.

Overall, we showed that differences in the volume of sampled vegetation did not significantly influence spider species richness probably due to differences in spider assemblages sampled by both methods used. This study showed that pitfall trap-based method is uncorrelated to litter sifting and, unknnot suitable to sample ground-dwelling spiders, probably due to a too high (large spiders) or too low (small species) mobility. The habitat type (i.e. lowland vs. inselberg) influenced the species richness and composition of tropical vegetation-dwelling spiders, probably due to harsher conditions on inselberg (no pattern was found for ground-dwelling spiders). This study is, to our knowledge, the first to compare composition of spider assemblages between lowland and inselberg forests using a standardized and statistically robust protocol. We showed the originality of inselbergs when compared to adjacent, lowland, assemblages, and bring out the basis for further studies on inselberg spider assemblages. The sampling period did not significantly influence the species richness of vegetation and ground-dwelling spiders, not more than the composition of assemblages, the latter being inconsistent with usually defined hunting guilds. Finally, by comparing vegetation and ground-dwelling spider assemblages, we showed that their diversities were not correlated, and that they differently responded to ecological factors such as habitat type. Further studies are needed to understand inselberg spider diversity, test some better standardized ground sampling in tropical rainforest, and assess the importance of other ecological factors such as vegetation structure, biomass, litter depth or prey density. Finally, this study suggests some particularities of spider assemblage structure and composition compared to the literature which is largely based on temperate habitats. It is thus urgent to compare factors shaping arthropod diversity and composition between tropical and habitats and using similar protocols.

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Supporting Information**Table S1.** Relative abundance of morpho-species collected in vegetation in inselberg and lowland forests (sweeping and beating).

Family	Morpho-species code	Inselberg (%)	Lowland (%)
Anapidae	Ana1	-	0.4
	Ana2	-	0.4
Anyphaenidae	Any1	0.8	1.7
	Any5	4.7	-
	Any6	1.6	-
	Any7	0.8	-
	Any10	-	0.4
	Any11	0.8	-
	Any12	-	0.4
	Any13	-	0.4
Araneidae	Ara2	5.5	-
	Ara4	0.8	-
	Ara10	0.8	-
	Ara11	0.8	-
	Ara13	1.6	-
	Ara15	0.8	-
	Ara19	0.8	-
	Ara20	1.6	-
	Ara21	0.8	-
	Ara22	0.8	-
	Ara23	0.8	1.3
	Ara24	-	0.4
	Ara25	-	3.9
	Ara26	-	0.4
	Ara28	0.8	0.4
	Ara30	-	0.4
	Ara31	-	0.9
	Ara33	-	2.2
	Ara34	-	0.9
	Ara35	-	0.4
	Ara36	-	0.4
	Ara37	-	0.4
	Ara39	-	0.9
	Ara40	-	1.3
	Ara41	-	0.9
	Ara42	0.8	0.4
	Ara45	-	0.4
Ara46	-	0.4	
Ara47	-	0.4	
Ara48	-	0.4	
Ara49	-	0.4	
Ara50	-	0.4	
Ara51	0.8	-	

Family	Morpho-species code	Inselberg (%)	Lowland (%)
	Ara52	0.8	-
	Ara53	0.8	0.4
	Ara54	0.8	-
	Ara55	0.8	-
	Ara57	0.8	-
	Ara58	0.8	0.9
	Ara59	-	0.4
	Ara60	-	0.4
	Ara61	-	0.4
	Ara62	-	0.4
	Ara63	-	0.4
	Ara66	-	0.4
	Ara67	0.8	0.4
	Ara69	3.1	-
	Ara70	-	0.4
	Ara72	-	0.9
	Ara73	-	0.4
	Ara74	-	0.4
Clubionidae	Clu2	-	0.9
	Clu3	0.8	-
Corinnidae	Cor3	-	5.2
	Cor4	0.8	-
	Cor5	-	0.4
	Cor7	-	0.4
Ctenidae	Cte3	-	1.3
	Cte4	-	0.9
	Cte5	-	0.9
Linyphiidae	Lin5	-	0.4
Mimetidae	Mim2	0.8	-
	Mim3	0.8	-
	Mim4	0.8	-
	Mim9	0.8	-
Nesticidae	Nest1	-	0.4
Oonopidae	Oon1	2.4	-
	Oon3	-	1.3
	Oon5	-	0.9
Pholcidae	Pho2	0.8	-
Scytodidae	Scy1	2.4	-
Salticidae	Amycus sp1	0.8	1.7
	Chira_sp1	-	0.4
	Chira_sp3	-	0.4
	Cotinusa_sp2	-	0.4
	Cylistella_sp1	7.9	3.9
	Cylistella_sp2	3.9	-
	Eustiromastix_guianae	0.8	-
	Gen14_sp1	-	0.4
	Gen18_sp1	0.8	-
	Gen19_sp2	0.8	-

Family	Morpho-species code	Inselberg (%)	Lowland (%)
	Gen20_sp1	-	0.4
	Hypaeus_sp2'	-	1.7
	Hypaeus_taczanowskii	4.7	2.2
	Lyssomanes_longipes	-	0.9
	Lyssomanes_sp5	-	0.4
	Mago_longidens	-	2.2
	Neogus_sp10	-	0.4
	Noegus_sp9	0.8	-
	Scopocira_sp1	-	0.9
	Sidusa_sp1	-	0.4
	Soesilarishius_aurifrons	-	0.4
	Soesilarishius_ruizi	-	0.4
	Soesilarishius_sp1	-	0.4
	Zuniga_magna	2.4	-
Sparassidae	Spa1	0.8	-
	Spa2	0.8	-
	Spa4	0.8	-
Synotaxidae	Syn3	-	0.9
	Syn7	-	0.4
Tetragnathidae	Tet3	0.8	-
	Tet4	-	2.2
	Tet6	0.8	-
	Tet7	-	0.4
	Tet9	0.8	0.4
	Tet10	-	0.4
Theridiidae	Ther4	0.8	0.4
	Ther5	0.8	0.9
	Ther8	-	1.3
	Ther10	3.9	0.9
	Ther12	0.8	-
	Ther16	-	2.2
	Ther17	-	0.4
	Ther18	0.8	3.1
	Ther20	-	0.9
	Ther21	-	0.9
	Ther22	-	0.4
	Ther23	-	0.4
	Ther24	-	0.4
	Ther25	-	0.4
	Ther29	-	0.4
	Ther30	-	0.4
	Ther32	-	0.4
	Ther39	-	0.4
	Ther41	-	0.4
	Ther42	-	0.4
	Ther43	-	0.4
	Ther45	-	0.4
	Ther46	-	0.4

Family	Morpho-species code	Inselberg (%)	Lowland (%)
	Ther48	0.8	-
	Ther50	0.8	-
	Ther51	0.8	-
	Ther55	-	0.9
	Ther56	-	0.4
	Ther57	-	0.4
	Ther59	-	0.4
	Ther60	-	0.9
	Ther61	-	0.4
	Ther62	-	0.4
	Ther63	-	0.4
	Ther64	-	0.4
	Ther65	-	0.4
Theridiosomatidae	Therio2	-	0.4
	Therio3	-	0.4
Thomisidae	Tho2	0.8	0.4
	Tho3	2.4	3.1
	Tho4	0.8	0.4
	Tho9	-	3.1
	Tho11	-	0.4
	Tho15	-	0.4
	Tho16	-	0.4
	Tho17	-	0.4
	Tho18	-	0.9
	Tho19	-	0.4
	Tho22	-	0.4
	ThoA	-	0.9
	ThoB	6.3	0.9
	ThoC	2.4	-
	ThoG	0.8	-
Uloboridae	U1	1.6	-
	U3	0.8	-
	U5	0.8	-
	U8	0.8	-
	U9	0.8	-

Table S2. Relative abundance of ground-dwelling morpho-species collected by litter sifting in inselberg and lowland.

Family	Morpho-species code	Inselberg	Lowland	
Anapidae	Ana1	-	10%	
	Ana2	-	5%	
Araneidae	Ara33	7%	-	
	Ara76	7%	-	
	Ara77	7%	5%	
	Ara78	-	5%	
	Corinidae	Cor8	-	5%
Ctenidae	Cor9	-	5%	
	Cte19	7%	-	
Dipluridae	Cte21	-	5%	
	Diplu1	-	10%	
Linyphiidae	Lin6	7%	-	
	Lin7	-	5%	
Oonopidae	Oon11	-	5%	
Palpimanidae	Palp2	7%	-	
Pholcidae	Pho5	-	5%	
	Sa22	7%	-	
	Sa27	7%	-	
	Sa33	7%	-	
	Salticidae	Sa40	7%	-
		Sa48	13	-
		Sa51	7%	-
		Sa55	7%	-
	Theridiidae	Ther68	7%	-
		Ther69	-	5%
Ther70		-	5%	
Ther71		-	5%	
Ther72		-	10%	
Ther73		-	5%	
Ther74		-	5%	

PART II : COMPLÉMENTARITÉ DES APPROCHES TRAITS ET TAXONS POUR LA COMPRÉHENSION DES PATTERNS DE DIVERSITÉ DES ARAIGNÉES TROPICALES

**COMMENT L'APPROCHE BASÉE SUR LES TRAITS PEUT-ELLE AIDER À
LA COMPRÉHENSION DES PATTERNS DE DIVERSITÉ DES ARAIGNÉES
TROPICALES ?**

CHAPITRE.3

Comparaison des patterns de diversité taxonomique et fonctionnelle des araignées entre forêts tropicales et tempérées

Comparative patterns in taxonomic and functional spider diversities between tropical vs. temperate forests

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Abstract

High diversity in tropical compared to temperate regions has long intrigued ecologists, especially for highly speciose taxa like terrestrial arthropods in tropical rainforests. Previous studies showed that arthropod herbivores account for much tropical diversity, yet differences in the diversity of predatory arthropods between tropical and temperate systems have not been properly quantified. Here, we present the first standardized tropical–temperate forest quantification of spider diversities, a dominant and mega-diverse taxon of generalist predators. Spider assemblages were collected using a spatially replicated protocol including two standardized sampling methods (vegetation sweep netting and beating). Fieldwork took place between 2010 and 2015 in metropolitan (Brittany) and overseas (French Guiana) French territories. We found no significant difference in functional diversity based on hunting guilds between temperate and tropical forests, while species richness was 13-82 times higher in tropical versus temperate forests. Evenness was also higher, with tropical assemblages up to 55 times more even than assemblages in temperate forests. These differences in diversity far surpass previous estimates and exceed tropical–temperate ratios for herbivorous taxa.

Key words: alpha diversity, Araneae, deciduous trees, France, French Guiana, functional diversity, intensive sampling.

Introduction

The latitudinal gradient of diversity, that is increase in species richness with decreasing latitude, has long been recognized by the scientific community (Pianka, 1966). Gradients of diversity in various arthropod taxa from tropical to temperate and even polar ecosystems are well documented through meta-analyses (Willig et al., 2003; but see Hillebrand, 2004). Arthropods were particularly studied in tropical rainforests (the species richest terrestrial ecosystem: Miller et al., 2002) where nearly 1.5 million tropical arthropod species are currently described out of an estimated number of 2 to 7 million tropical arthropod species (Hamilton et al., 2010; Stork, 2017). Herbivorous arthropod assemblages have been extensively studied in both tropical and temperate forests with studies of diversity, species richness per plant, host specificity, and herbivory pressure. Herbivore arthropod diversity, as well as rate of herbivory, are considered higher in tropical systems compared to temperate counterparts (Lim et al., 2015; Peguero et al., 2017), though evidence of greater host specificity is still controversial (Novotny, 2006; Peguero et al., 2017). Such gradients in herbivore diversity can be explained by underlying plant diversity, herbivore diet specialization, and plant defense. Less well studied is the possible role of natural enemies (i.e., predators and parasitoids) on herbivore arthropod diversity (Björkman et al., 2011). Latitudinal gradients in the diversity of omnivore arthropods have also been studied, mainly in ants for which assemblages are clearly species richer in tropical versus temperate systems (Jaffre et al., 2007; Jeanne, 1979). For example, canopy assemblages of ants from tropical forests are estimated to be 4 times richer than those from temperate forests (Jaffre et al., 2007). Although ants are considered the main predatory arthropods in tropical rainforests (Floren et al., 2002), they complete a large variety of functional roles (Dejean & Corbara, 2003), and their diversity thus does not reflect the diversity of predatory arthropod taxa.

Few studies have examined the latitudinal gradient of predatory arthropod diversity, while other macro-ecological patterns were investigated in these taxa (e.g., for spiders: Arvidsson et al., 2016; Finch et al., 2008; Kozlov et al., 2015; Pitta et al., 2019; Ysnel et al., 2008). To date, most of the studies focused on predation pressure, for example, highlighting that predation pressure increases when latitude decreases (Andrew & Hughes, 2005; Novotny, 2006; Rodríguez-Castañeda, 2013), but sometimes remains constant (Cardoso et al., 2011; Zhang & Adams, 2011). Lacking are studies that directly compare the diversity of tropical versus temperate for predatory arthropods (Schuldt et al., 2013), despite their strong contribution to ecosystem diversity and functioning (Björkman et al., 2011).

To the best of our knowledge, only one study has evaluated and quantified the difference of tropical versus temperate diversity in predatory arthropods. It was conducted by Basset et al. (2012) who performed a comparison of tropical and temperate forests for different trophic guilds based on data obtained independently, using different sampling protocols. They estimated that differences in predatory arthropod diversity between tropical and temperate ecosystems should be in the same range as those for herbivorous arthropods, with tropical assemblages being 2 to 8.4 times more diverse compared to temperate forest (Basset et al.,

2012). Although spiders constitute a relevant model taxon to compare predatory arthropods between temperate and tropical regions, this ratio has never been tested nor confirmed using spiders only. They are indeed one of the few taxa, if any other, that is exclusively, except for one species and occasional plant consumption by few other species (see the recent review by Nyffeler et al., 2016), composed by predatory species (Birkhofer & Wolters, 2012).

We present here the first standardized tropical–temperate quantification for vegetation-dwelling spider diversity using the same spatially and method-replicated sampling protocol. More specifically, we compared patterns of both taxonomic and functional diversities as they bring complementary information on ecological and evolutionary processes (Tucker et al., 2018). We first expected (a) correlated patterns between taxonomic and functional diversities (as previously documented in plants and vertebrates: see Tucker & Cadotte, 2013, but also in arthropods, e.g., Birkhofer et al., 2015 and Ridel et al., 2020), (b) consistently (much) more diversity and evenness in tropical compared to temperate forests due a longer time of diversification processes leading to more species and traits co-existence, and (c) an order of magnitude between temperate and tropical forests in the same range than what previously reported for other arthropods, that is, diversity and evenness around 8 times higher in tropical compared to temperate forests.

Methods

Study sites

Tropical and temperate sampling were replicated in both locations and sampling methods, to increase generalization power (Willis & Whittaker, 2002).

The two replicated tropical sites were two nature reserves in French Guiana (South America) sharing similar climates: La Trinité Reserve (76,900 ha; 4°35'2"N, 53°18'1"W) and Nouragues Reserve (105,000 ha; 4°04'18"N, 52°43'57"W). These sites are seasonally flooded rainforests with representative vegetation of the primary lowland rainforest, with few inclusions of palmetto–swamp forests, liana forests, and bamboo forests. Both forests were sampled during the rainy season, considered as the period of maximum diversity in tropical forests (e.g., Gasnier & Höfer, 2001). La Trinité and Les Nouragues were hereafter called tropical forest one and tropical forest two, respectively.

Temperate sites were in two forests preserves of mixed hardwood forests in Brittany (Western France): the forest of the military camp of Saint-Cyr-Coëtquidan (2,000 ha; 47°57'50"N, 2°11'30"W) and the state-owned forest of Rennes (3,000 ha; 48°11'53"N, 1°33'22"W). The vegetation of these forests is representative of many temperate forests with some shrubby species, small trees, and climbing plants. Only forest types dominated by native deciduous trees were sampled. Both forests were sampled in summer, the period estimated to have maximal spider diversity (see Hsieh & Linsenmair, 2012). Saint-Cyr-Coëtquidan and Rennes were hereafter called temperate forest one and temperate forest two, respectively.

While the actual sampled area was similar in all four forests, we consider the size of studied forests to be a confounding factor and an intrinsic part of the difference between tropical and temperate forests, as there are anyway no temperate forests as big as the Amazonian forest, to which the two tropical Nature Reserves sampled here belong. Tree species richness is also an intrinsic difference between the forests in each biome, with around 150 species in both Trinité and Les Nouragues tropical forests (see Guitet et al., 2018 and Poncy et al., 1998, respectively), and 10 times less in Rennes and Coëtquidan temperate forests (V. Jung comm. pers. and Morel et al., 2020, respectively).

Sampling and identification

We developed a quasi-optimal protocol (sensu Malumbres-Olarte et al., 2017 who defined it as a “standardized protocol that may not be optimal for any specific site alone.”) designed for short and intensive surveys. In each forest, we used two surface-standardized active sampling methods highly efficient for vegetation-dwelling spiders (Coddington et al., 2009): beating and sweep netting. Vegetation beating was conducted in 9 × 9 m quadrats where the vegetation was beaten with a stick over a beating tray to a height of 2.5 m. In each forest, 12 randomly selected quadrats were conducted by four people in two duos concurrently (six quadrats per duo). Sweep netting was carried out with a sweep net along 20 m long and one-meter-wide (arm length plus sweep handle) transects. Twelve randomly selected transects were conducted in each forest by the same two persons. All quadrats and transects were carried out in visually homogeneous areas of each forest that differed between methods. Tropical forest one was sampled 3–7 December 2010, tropical forest two, 6–15 December 2013, temperate forest one, 15–16 June 2015, and temperate forest two, 22–23 June 2015. Temperate adult spiders were sorted and identified to species, while tropical adult spiders were identified to morphospecies because of a lack of taxonomic knowledge in the tropics (Scharff et al., 2003). Whenever possible, males and females were matched together and grouped into one single morphospecies. All specimens were identified by the authors and stored at the University of Rennes 1, France.

Data analysis

Because limited information for tropical spiders, functional metrics was based on abundance of family hunting guilds only (Cardoso et al., 2011), using FD R package on the Gower dissimilarity matrix with a Cailliez correction (Laliberté et al., 2014).

The difference between functional diversity and evenness observed in each biome with each sampling technique was assessed using a mixed linear model with a Gaussian distribution. Functional diversity and evenness were the response variables, and biome and site were the predictors (respectively, fixed and random factors). Normality of results was checked using diagnostic plots. We standardized the comparison of taxonomic diversity between the four forests by using species rarefaction and extrapolation curves based on sample coverage (Chao et al., 2014). Analyses were completed using the R-based iNEXT

package (Chao et al., 2014) with R Software (R Development Core Team, 2018) on summed species abundances over the 12 replicates per method and per site. iNEXT function was configured at 40 knots and 200 bootstraps replications. 95% confidence intervals (CI) were calculated for the three measures of species diversity (species richness, Shannon, and Simpson diversity indices) within overlap of CI used to indicate a significant difference at a level of 5% among the expected diversities (Chao et al., 2014). Diversities were compared at the same sample coverage (named “base coverage”), following Chao et al. (2014), allowing for a standardized comparison of spider assemblage diversity between biomes despite differences in forest areas. Comparisons were conducted at 38.8% sample coverage for beating and at 60% sample coverage for sweep netting.

Results

A total of 2,846 individuals belonging to 202 (morpho-)species were collected (see detailed taxonomic list: [Table S1](#)).

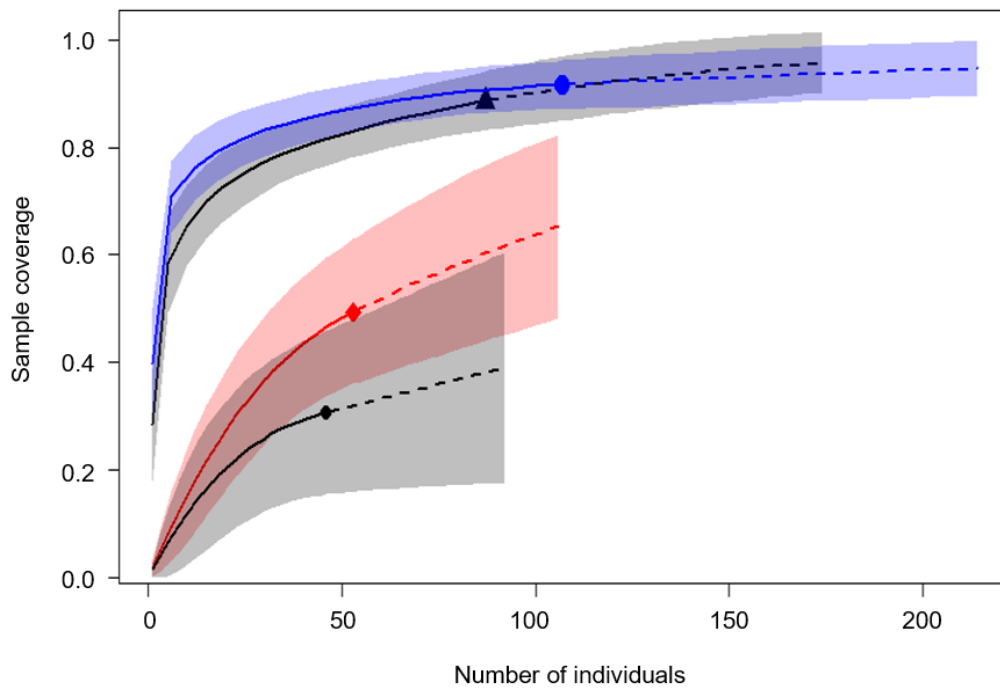
No significant differences were found between models of functional diversity based on beating sampling ($t = -0.082$, $df = 1.3$, $p = .529$) or based on sweep netting ($t = 26.06$, $df = 1.9$, $p = .195$), indicating an absence of a biome effect. The same was found for functional evenness, that is, no significant effect of biome on this metric by beating ($t = 0.79$, $df = 1.92$, $p = .515$) and by sweep netting ($t = 2.84$, $df = 1.96$, $p = .107$).

Based on rarefaction, the sample coverage was nearly two times higher in temperate forests for the two sampling methods and almost any sample size (i.e., number of individuals; [Figure 1a, b](#)). When comparing samples at the same effective sample size for both methods, sample coverage was about 90% in temperate and between 30% and 53% in tropical forests. Thus, even though the same standardized protocol was used in both biomes, temperate samples were two to three times more complete than tropical ones. Based on the extrapolation for both sampling methods, when the sample size was doubled, the sample coverage increased by three to seven percent for temperate forests and by nine to 16% in tropical ones ([Figure 1a, b](#)).

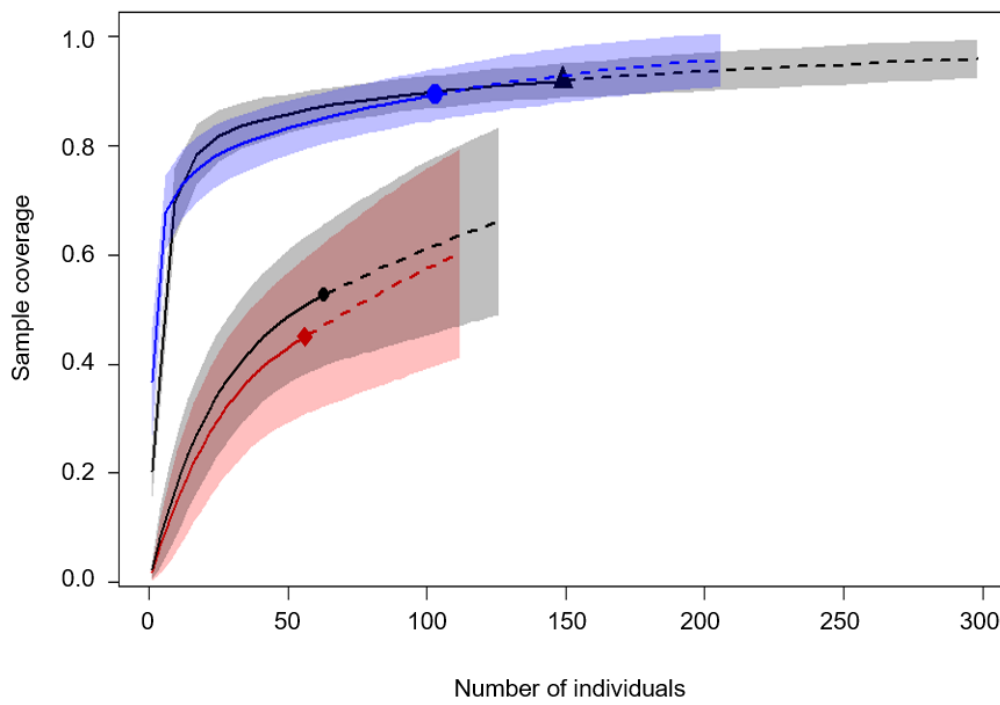
When comparing coverage-based diversities of tropical and temperate forests at the same sample coverages, confidence bands of the replicated sites of tropical and temperate forests did not overlap for either beating or sweep netting ([Figures 2 and 3](#)). Thus, tropical spider assemblages were highly and significantly more diverse than temperate ones for any sample coverage, sampling method, and diversity indices used (see detailed results below).

Beating and sweep netting consistently showed the same patterns. Tropical spider assemblages were 12.9 to 81.6 times species richer than temperate ones ([Figures 2 and 3](#)). Difference in diversity between biomes was also significant for Shannon diversity and for Simpson diversity. Shannon diversity was 11.6 to 54.6 times higher in tropical assemblages than in temperate counterparts, and Simpson diversity was 10.4 to 40.4 times higher in tropical assemblages ([Figures 2 and 3](#)).

(a) Sampling method 1



(b) Sampling method 2



● Tropical forest 1 ◆ Tropical forest 2 ▲ Temperate forest 1 ● Temperate forest 2

Figure 1: Sample coverage for rarefied samples (solid line) and extrapolated samples (dashed line) as a function of sample size for spider samples collected by (A) sampling method one (beating) and (B) sampling method two (sweep netting) in tropical rainforests one and two (La Trinité and Les Nouragues) and the temperate deciduous forests one and two (Coëtquidan and Rennes). The 95% confidence intervals

are represented in light color and were obtained by a bootstrap method (Chao et al. 2014) based on 200 replications. Reference samples in each forest are denoted by solid markers. For comparison, all curves were extrapolated up to double its reference sample size. The numbers in parentheses are the sample coverage and the number of individuals for reference samples.

Discussion

Using a spatially and method-replicated protocol, we found that the taxonomic diversity of spiders was much higher in tropical forests compared to temperate forests (with consistent patterns for all diversity metrics and for the two sampling methods), when no difference was detected for functional diversity.

The fact that functional diversity was not differing among biomes can indicate either similar levels of or balanced effects of both habitat filtering and interspecific competition (Fichaux et al., 2019), which would be especially interesting at such a large spatial scale. Phylogenetic diversity can also be an interesting side of diversity, which might not be correlated with taxonomic and functional diversities as well (Tucker et al., 2018). Cardoso et al. (2011) also suspected spider taxonomic diversity to be higher in the tropics, but with species functionally redundant, which was supported by Schuldt et al. (2013) who compared tropical (China) and temperate (Germany) spider assemblages.

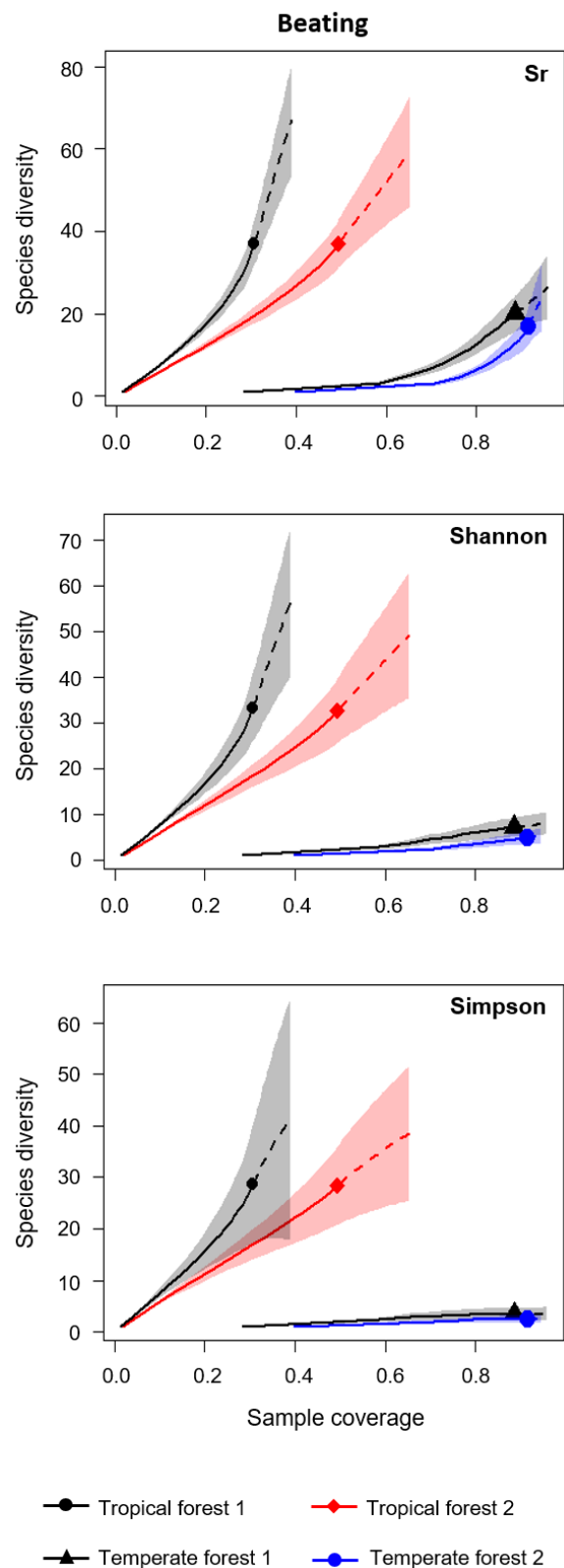


Figure 2: Comparison of the coverage-based rarefaction (solid line) and extrapolation (dashed line) of spider (A) species richness (Sr), (B) Shannon diversity and (C) Simpson diversity collected by sampling method one (beating) in tropical rainforests one and two (La Trinité and Les Nouragues) and the temperate deciduous forests one and two (Coëtquidan and Rennes). The 95% confidence intervals are represented in light color and were obtained by a bootstrap method (Chao et al. 2014) based on 200 replications. Reference samples in each forest are denoted by solid markers. For comparison, all curves were extrapolated up to double its reference sample size. The numbers in parentheses are the sample coverage and the observed diversity indices (species richness, Shannon or Simpson) for each reference sample.

The functional diversity was yet based on hunting guilds only in this study and should be computed with other traits in the future when they will be available at large spatial scales (Lowe et al., 2020).

Our study showed that, with the same level of sample coverage, species richness of tropical forest spiders was 13–82 times higher than temperate species richness. This magnitude of difference is much greater than expected (i.e., two to eight times more than in Basset et al., 2012). The comparison of evenness also revealed that the spider assemblages we sampled in tropical forests were also up to 55 times more even than in temperate forests. Weighted measures of diversity (i.e., species evenness and species dominance) are known to provide more comprehensive views of patterns of taxonomic diversity (Willig et al., 2003). Diversity metrics responded in the same way than species richness (and consistently between sampling methods), which confirms that spider diversity was up to 30 times higher than what was previously proposed for predatory arthropods through indirect comparisons.

Although several methodological factors could influence the difference in ratios between Basset et al. (2012) and this study, and among them the indirect comparison used by Basset et al. (2012), the strata sampled (understory here vs. soil to canopy for Basset et al., 2012), and the species richness estimation methods (a large range of different estimators in Basset et al., 2012) but without considering sample

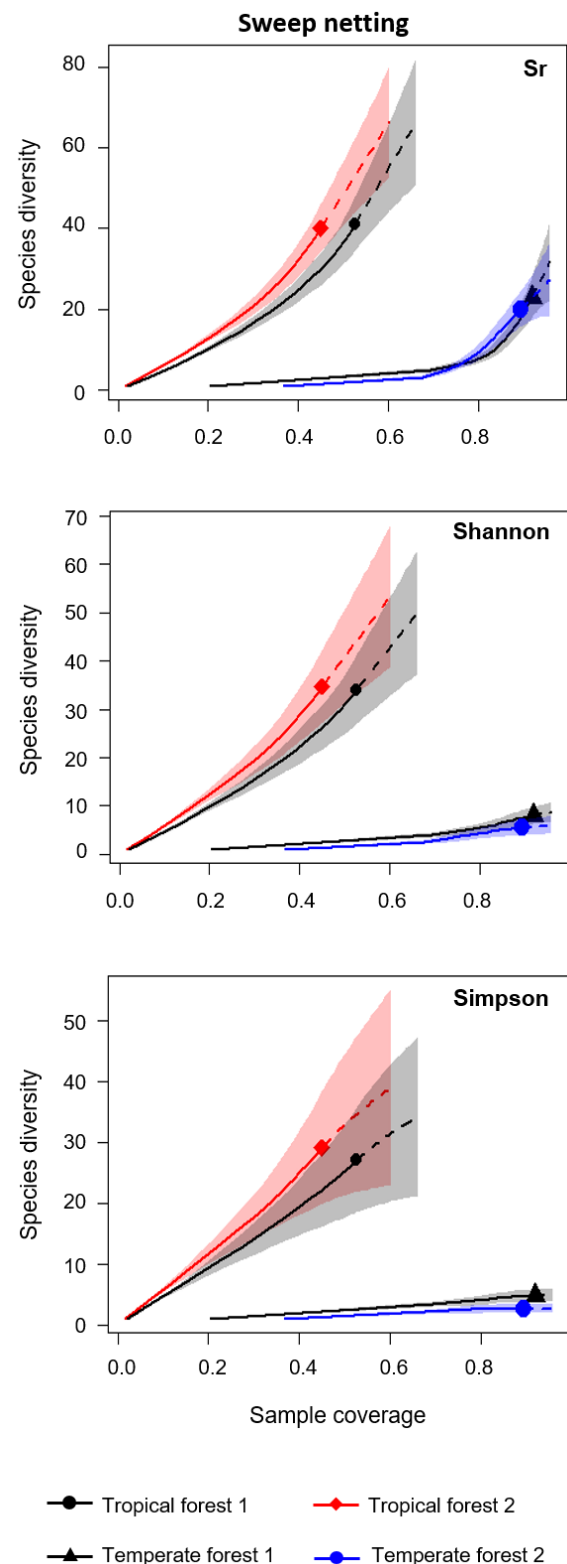


Figure 3: Comparison of the coverage-based rarefaction (solid line) and extrapolation (dashed line) of spider (A) species richness (Sr), (B) Shannon diversity and (C) Simpson diversity collected by sampling method two (sweeping) in tropical rainforests one and two (La Trinité and Les Nouragues) and the temperate deciduous forests one and two (Coëtquidan and Rennes). The 95% confidence intervals are represented in light color and were obtained by a bootstrap method (Chao et al. 2014) based on 200 replications. Reference samples in each forest are denoted by solid markers. For comparison, all curves were extrapolated up to double its reference sample size. The numbers in parentheses are the sample coverage and the observed diversity indices (species richness, Shannon or Simpson) for each reference sample.

coverage), we still argue that predatory arthropods are proportionally more diverse in tropical compared to temperate forests than other taxa, like, for example, herbivore arthropods and plants. The global difference in diversity between tropical and temperate ecosystems is indeed partly explained by both plant species richness and plant phylogenetic diversity (Dinnage et al., 2012), which suggests that the diversity of predatory arthropods also mirrors plant diversity. Interestingly, the values of tree diversity of our study sites are comparable to those of other temperate and neotropical forests (see e.g., Brokaw & Busing, 2000) and also fit to previous estimations of 5–10 times more plant species per hectare in tropical compared to temperate areas (Barthlott et al., 1996). Hence, the 13–82 times higher species richness of spiders in tropical rainforest would be vastly higher than the actual difference in tree diversity between the same pairs of forests. Thus, spiders would be 1.2 to 16 times proportionally richer than plants in tropical compared to temperate systems. These results suggest that the relationship between spider and plant diversity in tropical forest would not be one-to-one as it was previously estimated for all trophic level arthropods (Basset et al., 2012; Dinnage et al., 2012). The ratio between plant and spider diversity in tropical forests compared to temperate forests could be higher due to a wider diet of spiders in tropical versus temperate forests (see Birkhofer & Wolters, 2012 for further information). Lastly, vegetation structure, known to affect spider diversity (see e.g., Hurd & Fagan, 1992), could also have played a role in shaping differences of species richness between biomes. But understory structure, that was not quantified here, did not look so different between (primary) tropical and (secondary) temperate forests, even possibly higher in the latter (K. Privet & J. Pétilion, pers. observations).

Finally, intensive sampling in tropical regions is often limited in time and replication, which potentially induces biases such as random effects and particular local conditions. We are aware that our design would have benefited from additional replication, but there is also a risk to increase intratreatment variance by doing so in a single design (Oksanen, 2001). Therefore, we encourage tropical researchers to continue sampling spider diversity, using this or other standardized sampling protocols, in paired comparisons of tropical versus temperate forests to infer on eco-evolutionary drivers of biodiversity patterns at large spatial scales.

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Supporting information

TABLE S1: List and abundances of species collected during this study. Part of the spiders collected in tropical forests were unknown and only tropical spiders belonging to the family Salticidae were identified to the species level.

Forest		Species	Abundance
Temperate forest (Saint-Cyr-Coëtquidan)	1	Anelosimus vittatus	1
		Araneus diadematus	1
		Ballus chalybicus	2
		Clubiona compta	4
		Clubiona terrestris	1
		Diaea dorsata	2
		Dipoena melanogaster	1
		Enoplognatha ovata	102
		Episinus maculipes	1
		Gongylidium rufipes	3
		Hypomma cornutum	2
		Linyphia hortensis	2
		Mangora acalypha	1
		Metellina menegi	31
		Metellina meriane	4
		Neottiura bimaculata	2
		Neriere peltata	1
		Neriere radiata	1
		Oedothorax fuscus	2
		Paidiscura pallens	2
		Parasteatoda simulans	2
		Pelecopsis parallela	1
		Philodromus albidus	2
		Philodromus rufus	1
		Platnickina tinctoria	2
		Porrhomma microphthalmum	1
		Tenuiphantes flavipes	33
		Tenuiphantes zimmermanni	14
		Tetragnatha montana	4
		Theridion varians	2
Theridiosoma gemmosum	4		
Zilla dioidia	4		
Temperate forest (Rennes)	2	Anelosimus vittatus	1
		Araneus diadematus	1
		Batyphantes gracilis	5
		Ceratinella scabrosa	1
		Clubiona brevipes	1
		Diaea dorsata	1
		Dipoena melanogaster	1
		Enoplognatha ovata	127
		Erigone atra	1

			<i>Erigone dentipalpis</i>	2
			<i>Hypomma cornutum</i>	1
			<i>Linyphia hortensis</i>	1
			<i>Metellina mengei</i>	17
			<i>Neriere peltata</i>	2
			<i>Nigma puella</i>	1
			<i>Oedothorax fuscus</i>	1
			<i>Oedothorax retusus</i>	1
			<i>Paidiscura pallens</i>	7
			<i>Parasteatoda lunata</i>	2
			<i>Parasteatoda simulans</i>	4
			<i>Philodromus albidus</i>	1
			<i>Philodromus dispar</i>	3
			<i>Philodromus praedatus</i>	1
			<i>Platnickina tincta</i>	14
			<i>Tenuiphantes flavipes</i>	5
			<i>Tenuiphantes tenuis</i>	1
			<i>Tenuiphantes zimmermanni</i>	2
			<i>Tetragnatha montana</i>	1
			<i>Tetragnatha obtusa</i>	2
			<i>Theridion varians</i>	1
			<i>Walckenaeria vigilax</i>	1
Tropical	forest	1		
(La Trinité)			AnaA	1
			AnaB	1
			AnyA	1
			AnyH	1
			AraAP	1
			AraAR	1
			AraAT	1
			AraC	1
			AraD	1
			AraE	1
			AraG	1
			AraH	1
			AraI	1
			AraJ	3
			AraL	1
			AraP	1
			AraV	1
			CluA	1
			Cobanus sp3	1
			CorA	1
			CorH	1
			CorJ	1
			CorK	1
			CorL	1
			CorM	1
			Corythalia sp4	1

Cylistella sp1	1
Erica eugenia	1
Gen9 sp1	1
Hypaeus porcatus	1
Hypaeus sp2'	3
Hypaeus taczanowskii	10
LinA	1
LinE	1
LinI	1
Lyssomanes longipes	2
Lyssomanes nigropictus	1
Lyssomanes sp3	1
Mago longidens	1
MimA	4
Noegus niveomarginatus	4
Noegus sp1	2
Noegus sp11	1
Noegus sp5	1
OxyoA	1
OxyoB	2
PhoIA	3
PisC	1
PisE	1
PisF	1
PisG	1
PisI	1
Scopocira cf tenella	3
ScyA	4
ScyB	1
ScyC	1
Soesilarishius sp1	1
TetF	1
TherAA	2
TherAF	1
TherAG	1
TherAH	1
TherAI	1
TherAJ	1
TherAK	1
TherAL	1
TherAQ	1
TherB	10
TherC	2
TherD	6
TherE	1
TherG	3
TherH	2
TherI	1

TherJ	2
TherK	2
ThoAD	1
ThoAE	1
ThoAF	2
ThoAK	1
ThoB	1
ThoC	10
ThoD	1
ThoE	6
ThoF	1
ThoH	6
ThoI	5
ThoJ	1
ThoN	1
ThoO	1
ThoP	5
ThoQ	1
UloA	2
UloD	4
UloJ	1
UloK	1
<hr/>	
Tropical forest	2
(Les Nouragues)	
Ana2	1
Any1	1
Any12	1
Any13	1
Ara23	2
Ara25	6
Ara33	4
Ara40	2
Ara53	1
Ara58	2
Ara59	1
Ara60	1
Ara61	1
Ara62	1
Ara63	1
Ara66	1
Ara72	2
Chira sp1	1
Cor3	5
Cor5	1
Cor7	1
Cotinusa sp2	1
Cylistella sp1	7
Gen20 sp1	1

Hypaeus sp2'	1
Hypaeus taczanowskii	5
Lin5	1
Mago longidens	4
Neogus sp10	1
Nest1	1
Oon5	2
Sidusa sp1	1
Soesilarishius aurifrons	1
Soesilarishius ruizi	1
Soesilarishius sp1	1
Syn3	1
Syn7	1
Tet10	1
Tet4	2
Tet7	1
Tet9	1
Ther10	1
Ther16	1
Ther18	3
Ther21	1
Ther55	2
Ther56	1
Ther57	1
Ther59	1
Ther60	2
Ther61	1
Ther62	1
Ther63	1
Ther64	1
Ther65	1
Therio2	1
Tho15	1
Tho16	1
Tho17	1
Tho18	2
Tho19	1
Tho2	1
Tho22	1
Tho3	5
Tho9	4
ThoA	1

CHAPITRE.4

Complémentarité des métriques basées sur les traits et sur les taxons pour comprendre les patterns de diversité tropicale – Un cas d'étude utilisant des assemblages d'araignées dans des habitats néotropicaux contrastés

Taxonomic and trait-based approaches help understanding tropical diversity – A case study using spider assemblages of French Guiana

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This article is in preparation

Abstract

To what extent taxonomic vs functional metrics are redundant in terms of revealing and understanding diversity patterns remains unclear, especially in purely predatory taxa. This question is highly relevant in tropical forests where arthropod assemblages reach huge species numbers and their assembly rules are still largely unknown. Using a large-scale design (gradient of forest structure repeatedly sampled in 4 sites distributed over French Guiana), we tested the redundancy between metrics of taxon- vs. trait-based diversities in spiders, a mega-diverse, yet less-studied, group of predatory arthropods. All spiders were identified to family level and then discriminated to morpho-species (described species whenever possible) based on both habitus and sexual organs to estimate taxonomic diversity (TD) to eventually compute three diversity metrics (q0-Species richness, q1-Shannon diversity, q2-Simpson diversity). Because the knowledge on traits is still scarce in spiders, we used the actual measurements of 6 biometric traits on all individuals to better estimate functional diversity (FD), together with the hunting guild of spiders (attributed to family level). We first tested for correlations between a first global set of diversity metrics (3 TD vs. 4 FD) using all possible combinations of traits. We then compared the patterns of estimated TD and FD (all for q0, q1 and q2) along with the range of habitat conditions (type of forest, type of localization and site), also investigating how patterns were affected by the presence/absence of juveniles in the dataset. Our results overall showed a little influence of including or not juveniles, a little influence of q order (except for increasing correlations between FD and TD metrics), a little influence of several traits (except for hunting guilds that drove most of the FD patterns) and conversely a strong influence of forest type on both TD and FD patterns which were globally correlated. While these results suggest important environmental filtering, even in tropical forests, the precise role of abiotic factors and the influence of species and traits in composition turn-over remain to be tested. Our study finally calls for better standardization of metrics, in terms of estimated metrics, but also for more actually-measured traits in arthropod community ecology.

Key words: Araneae, environmental filtering, estimated predictors, functional traits, French Guiana.

Introduction

Determining assembly rules of co-occurring species persists as a fundamental goal in community ecology (Weiher & Keddy, 2001). Assemblage diversity is influenced by both deterministic (i.e. niche related) and stochastic (i.e. neutral) factors. From the deterministic perspective, both biotic and abiotic factors locally influence the patterns of diversity (Weiher & Keddy, 2001; Maire et al., 2012) through niche differentiation (MacArthur & Levins, 1967) and habitat filtering (Keddy, 1992), respectively. Habitat filtering limits the establishment of species unable to tolerate abiotic conditions of a given habitat, resulting in co-occurring species with similar ecological attributes (Keddy, 1992). Competitive interactions can reduce the coexistence of species sharing similar niches (MacArthur & Levins, 1967) or reinforce competitive hierarchies of species (Chesson, 2000; Kunstler et al., 2012), resulting in niche differentiation through character displacement: spatial and/or temporal partitioning of species with similar ecological attributes (Diamonds, 1975; Gotelli & McCabe, 2002). Those deterministic processes act at different spatial scales such as local and regional scales (Chase & Myers, 2011). Simultaneously, assemblages are influenced by factors that are more stochastic such as chance colonization, random extinction, and ecological drift (Chase & Myers, 2011).

Traditionally, studies investigating assembly rules across different ecosystems focused mainly on taxonomic diversity. Taxonomic diversity does not give any information on character displacement, a change that occurs when similar species inhabit the same environment, and when natural selection favors the divergence in the characters (morphology, ecology, behavior, or physiology) of the organisms. A more comprehensive functional trait-based approach has recently been formalized, which links taxonomic entities with the ecological functions they fulfill in their environment, providing a means of distinguishing between assembly processes (McGill et al., 2006; Cadotte et al., 2011; Houseman & Gross, 2011; Villéger et al., 2011; Weiher et al., 2011). Integrating taxonomic and functional approaches thus provides a more comprehensive insight into the role of environmental filtering and competitive exclusion.

Arthropods are more and more investigated in ecological studies because of their huge abundance and diversity (Erwin, 1982; Scharff et al., 2003) as well as their central role in ecosystem functioning (Lamarre et al., 2012; Hamilton et al., 2013). A better understanding of the distribution patterns of arthropods is essential both to better predict the dynamics of their taxonomic and functional diversity and to manage efficiently the conservation issues related to these organisms (Novotny & Basset 2000). The majority of terrestrial eukaryote diversity on Earth is represented by arthropods in tropical rainforests (Miller et al., 2002; Hamilton et al., 2010). However, the rules that structure their assemblage across environmental gradients are still very little known (but see Lamarre et al., 2016; Fichaux et al., 2019; Privet et al., 2020). Determining how assemblages are structured across environmental gradients in tropical environments will help to understand the mechanisms that rule hyperdiverse communities. The taxonomic approach is complicated to use in tropical assemblages due to the lack of

knowledge of the species, and its only use has proven its limits to explain the patterns of diversity (e.g. Privet et al., 2018). Trait-based approaches give a complementary view of the patterns of diversity (Violle et al., 2007; Pavoine & Bonsall, 2011; Brousseau et al., 2018; Wong et al., 2019) and are increasingly being used to test mechanisms underlying assemblages (Moretti et al., 2017). Terrestrial arthropods constitute one of the most promising, but also challenging, taxa regarding community ecology (and underlying assembly rules), due to their huge taxonomic and functional diversity (Moretti et al., 2017). However, the trait-based approach is just starting to be unified for terrestrial arthropods (Brousseau et al., 2018; Wong et al., 2019; Lowe et al., 2020) and is especially hard to use in tropical environments due to the lack of knowledge in natural history including easy-to-measure functional traits. Interestingly, the growing number of studies comparing the patterns and drivers of taxonomic vs functional diversities for terrestrial arthropods show evidence for important differences among taxa (Hacala et al., 2021) and/or spatial scales (Privet & Pétilion, 2020) that prevent generalizations.

Among terrestrial arthropods, spiders (Araneae) are one of the most diversified and abundant groups with very large ecological affinities and a worldwide repartition. Due to these characteristics, spiders have been proposed as a model group for uncovering ecological patterns (Cardoso et al., 2011; Birkhofer & Wolters, 2012; Malumbres-Olarte et al., 2018). Spider assemblages are known to be determined by environmental factors (e.g. elevation, temperature, habitat structure and complexity) and biotic interactions (e.g., competition, intraguild predation, predation) in temperate ecosystems (but see Fernandez-Fournier & Avilés, 2018 for tropical habitats) assessed mostly by traditional taxonomic approach (Wise, 1993; Butler & Haddad, 2011; Gonçalves-Souza et al., 2011; Diehl et al., 2013; Malumbres-Olarte et al., 2013; Gómez et al., 2016; Mammola et al., 2016; Petcharad et al., 2016). The trait-based approach of assemblages is relatively new in spiders and has been recently taken to another level thanks to the creation of the World Spider Trait database (Lowe et al., 2020; Pekar et al., 2021, Pekar et al. in press). The diversity of spider traits is known to be influenced by, among other factors, habitat and vegetation structure (e.g. Schirmel et al., 2012; Corcuera et al., 2016; Gallé et al., 2018). However, knowledge on their traits is for the moment still lacking because individual traits are unreported, often derived from large-scale databases (Pey et al., 2014), or vary in an unquantified way (Basset et al., 2003), including at intraspecific scale (Suter & Benson, 2014). Moreover, spider traits functionality has not been explicitly tested (as for most terrestrial arthropods, Wong et al., 2019). Therefore, it is preferable to speak of trait-based diversity rather than functional diversity.

While trait-based diversity is known to be correlated to taxonomic diversity as a rule, first by mathematical effects (plants: Pavoine et al., 2013, spiders: Ridel et al., 2021), the redundancy of taxonomic vs trait-based (functional) diversity metrics in terms of revealing and understanding diversity patterns remains unclear, especially in purely predatory taxa. In this study, we investigated the variation of taxonomic and trait-based diversities of tropical spider assemblages over a range of tropical habitats varying in vegetation structure and

environmental constraints (Baraloto et al., 2011; Lamarre et al., 2016, see Material and methods for a description of the habitats). We therefore expected taxonomic and trait-based diversities to vary among habitats because of differences in environmental constraints, resource availability, plant composition and habitat structure (Lamarre et al., 2016). We present here preliminary results investigating the correlation of a set of diversity metrics, we first tested for direct correlations between three taxon-based vs. four traits-based diversity metrics using all possible combinations of seven traits (of which six were actually measured on spiders and one derived from literature). We then compared the patterns of estimated taxonomic and trait-based diversities along with the range of habitat conditions (type of forest, type of localization and site). Juveniles spiders are usually discarded from assemblage analysis due to the difficulty or impossibility to identify them (Coddington et al., 1996; Dobyns, 1997; Scharff et al., 2003). However, they constitute a significant part of the assemblages (eg) and their patterns are in some cases different than those of adults (Norris, 1999; Domènech et al., 2021) and similar in other (Jiménez-Valverde & Lobo, 2006). In tropical assemblages they can account from 40% (in Privet et al., 2020), to 67% (in Privet et al., 2018) or even 86% (in Campuzano et al., 2016). Thus we investigated the patterns of taxonomic and trait-based diversity of adults and juveniles assemblages.

Material and methods

Study sites

This study was conducted in four sites of French Guiana that represent the entire range of variation in climatic, edaphic, forest structure factors and forest habitats observed in a larger plot network in tropical forests of South America in Loreto, Peru, and French Guiana (Baraloto et al., 2011; Lamarre et al., 2016). Two sites were located along the coast of French Guiana: (1) the French Guiana Space Center (CSG) (5°13'51" N, 52°46'08" W), which is a protected that contains several habitats including diverse forests, savannahs, marshes and mangroves (CNES & ONF, 2020); and (2) Laussat (5°29'00" N, 53°34'00" W), which is mostly covered with plains forests (Guitet et al., 2015). The two other sites were located deeper inland: (3) La Trinité (4°35'20" N, 53°18'01" W) is a reserve situated on the center-north of French Guiana. It is covered with a variety of forests, crossed by a mountain range comprising multiple inselbergs (Réserve Naturelle La Trinité, 2013). (4) Les Nouragues (4°04'18" N, 52°43'57" W), is a reserve located in the center-east of French Guiana. It holds a large forest cover, rock savannahs and inselbergs (Réserve Naturelle Nouragues, 2013).

Each plot consisted of ten 10*50 m transects distributed in a 2-ha area chosen for homogeneity and representativeness of the habitat (Lamarre et al., 2016), and contained at least 60 trees. Environmental variables describing climate, soil and forest structure were used to define the environmental conditions of each studied plot (for complete details, see Baraloto

et al., 2011). Each habitat type was separated by 1km to avoid collecting specimens from adjacent habitats.

Studied habitats

We studied four of the main tropical habitats of the Amazon basin:

(1) Terra firme forests, which are the most common forest in French Guiana developing on high soil nutrient content. They are dense and stratified, with a typical forest canopy reaching 20 to 40 meters, dense shrub vegetation but a sparse herbaceous stratum (Baraloto et al., 2011).

(2) Seasonally flooded forests, which are regularly subject to inundations that submerge soil surfaces during periods of high precipitations (Baraloto et al., 2007). These repeated disturbances result in a high rate of tree fall which prevents plant succession (Ferry et al., 2010; Baraloto et al., 2011; Quesada et al., 2012). Their canopy is more open than in terra firme forests and only a few plant species are endemic to these seasonally flooded forests (Guitet et al., 2015)

(3) White sand forests, which develop over nutrient-poor and dry sandy soils. They have more open canopy than previously cited habitats and hold poorer amounts of organic matter although they have the highest wood density (Baraloto et al., 2011). White sand forests occur as habitat islands surrounded by Terra Firme and seasonally flooded forests (Fine & Bruna, 2016). They host endemic plant species (Fine et al., 2010).

(4) Inselberg forests, which grow over rocky, granitic formations so-called inselbergs. These forests are subject to harsh abiotic conditions, such as extreme temperatures or massive runoffs depleting soils of their nutrients. Inselberg forests have a dense herbaceous cover which is however dotted by sand and granite outcrops. Their vegetation is mostly composed of shrubs and thickets making their canopy widely open. Tree species richness of inselbergs forests was estimated equivalent to white sands forests tree species richness (see Baraloto et al., 2011 and Sarthou et al., 2009) but their vegetation is highly endemic (Porembski & Barthlott, 2000; Porembski, 2007).

Sampling

Fieldwork was conducted during 12 months between November 2013 and October 2015.

Spiders were sampled in 23 forests plots distributed among the four habitats (terra firme and seasonally flooded forests in all sites, white sand forests in coastal sites and inselberg forests: see Baraloto et al., 2011). Each plot consisted of ten 10*50 m transects distributed in a 2 ha area chosen for homogeneity and representativeness of the habitat (Lamarre et al., 2016), and contained at least 60 trees. Plots were at least 1 km apart to avoid interactions. Two plots were sampled into each habitat of each site, except the inselberg and the seasonally flooded forests of Les Nouragues and the inselberg forests of La Trinité where one plot was

sampled, and the terra firme forest of La Trinité where three plots were sampled, resulting in a total of 23 sampling plots.

Spiders were sampled using Amazonas traps in inland sites and using hand collecting in coastal sites. Amazonas traps consist of slipping a bag onto a plant before mightily shaking the tree to shake off the spiders, before collecting them utilizing aspirators (see Lopes et al., 2019 for details). Collected spiders were preserved in 70% ethanol and deposited at the Université of Rennes 1 (Rennes, France).

Taxonomic identification

Individuals were sorted and identified to family following to Dippenaar-Schoeman & Jocqué (1997), Adis (2001) and Jocqué et al. (2006). Due to the lack of taxonomical knowledge about tropical spiders, we thus identified spiders to morpho-species based on morphological traits, mainly by observation of genitalia and habitus. Under a 65 microscope, we realized a side-by-side comparison of specimens to determine distinct morphological entities. Both juveniles and adults were identified at the family level and tentatively at the morpho-species level when possible (down to species for salticids).

Traits selection and determination

We examined variation in hunting guilds and a suite of six morphological traits for spiders from the different forest habitats. This character set was selected a priori based on their importance to spiders use of the habitat.

Hunting guilds are non-phylogenetic groups of species that share one or a series of resources (Blondel, 2003) and may thus reflect the ecological niche of spiders. Hunting guilds were determined for families or genera according to Dias et al. (2009) and Cardoso et al. (2011) resulting in seven groups: active hunter, ambusher, stalker, ground web weaver, sheet web weaver, spatial web weaver, and orb web weaver.

Morphological traits were selected for their accessibility and their potential to reflect the use of the habitat by spiders: **leg length** may reflect efficiency in locomotion, dispersal, and web construction (Foellmer & Fairbairn, 2005; Foelix, 2010), and **body size** may reflect differences in environmental factors as it is with many life history mechanisms as resource use, starvation, desiccation resistance, and other physiological processes (Cushman et al., 1993; Entling et al., 2010). In total, **six measures** were realized to the nearest 0.001 mm using the software Fiji (Schindelin et al., 2012) and a binocular loupe equipped with a Nikon SMZ800 camera. The femurs of legs 1 and 4 (from the rim of the trochanter to the junction with the patella) and tibiae of legs 1 and 4 (from the rim of the patella to the junction with the metatarsus) were measured as indicators of leg lengths. When it was possible, these two legs were measured on the right side of spiders. The length of the prosoma (measured from the middle of its anterior extremity to the middle of its posterior extremity, dorsal view) and the width of the prosoma (measured at its widest, dorsal view) were measured as indicators of body size. As both measures were strongly correlated (85.03%), we realized analyses on

prosoma width only (Jakob et al., 1996). In case of a missing value (e.g. no legs), the individual received an average value of measured traits from the same morpho-species in the given plot, if any.

Diversity metrics and data analysis

As trait-based diversity is still under recent development in spiders (Lowe et al., 2020), we first tested direct correlations between taxon-based vs. traits-based diversity of the 7 possible combinations of the 3 non-correlated studied traits (hunting guilds, body size and leg length: see above). We explored the Spearman correlation of taxonomic diversity with trait-based diversity for three taxonomic diversity indexes – taxonomic richness, Shannon and Simpson diversity – and four trait-based (functional) diversity indexes – functional richness, functional evenness, functional divergence and Rao Index. (i) functional richness (FRic) indicates the amount of the functional space occupied by the community, (ii) functional evenness (FEve) describes regularity in the distribution of the community abundance within the functional trait space, (iii) functional divergence (FDiv) defines how species abundances are distributed within the functional trait space, and (iv) Rao index (RaoQ) measures dissimilarity between species divided by their relative abundances (Mason et al., 2005; Villéger et al., 2011). These trait-based diversity indexes were calculated following Botta-Dukát (2005) and Laliberté & Legendre (2010) methods, using the “dbFD” function in the “FD” package (Laliberté et al., 2014). The number of dimensions retained was equivalent to the number of species in the most species-poor community.

In a second step, we compared the patterns of taxonomic and trait-based diversities between habitats. We started by analyzing taxonomic diversity separately for inland and coastal sites. We then estimated both taxonomic and trait-based diversity (using all traits) for the pooled inland and coastal sites, and compared patterns over habitat types for adults only, juveniles only, and both. Taxonomic and trait-based diversities were estimated using rarefaction and extrapolation of hill numbers (Chao & Jost, 2012; Colwell et al., 2012; Chao et al., 2014, 2021; Hsieh et al., 2016). Hill numbers are a mathematically unified family of diversity indices that have been generalized for taxonomic and trait-based diversity (Chao et al., 2021). Hill numbers differ among themselves only by an exponent q . For taxonomic diversity, hill number of $q=0$ corresponds to the taxonomic richness; $q=1$ to the exponential of Shannon entropy (that can be interpreted as the effective number of abundant/common species); and $q=2$ to the inverse of the Simpson concentration index (that can be interpreted as the effective number of highly abundant or dominant species). For trait-based (functional) diversity, hill number of $q=0$ corresponds to the effective total number of functional groups (functional-group richness); $q=1$ to the effective number of common/abundant functional groups; and $q=2$ to the effective number of dominant or highly abundant functional groups (Chao et al., 2021). Comparisons of estimated diversities can be made at the same sample size (comparisons based on the number of individuals) or the same sampling coverage (comparisons based on the sample completeness). The sample size does not take into account the fact that some assemblages are richer than others and therefore leads to an

underestimation of large assemblages (Chao & Jost, 2012). Sampling completeness represents the proportion of assemblage species represented in a sample (Chao & Jost, 2012). Comparing estimated assemblage diversity based on completeness recognizes that more diverse assemblages require greater sampling effort to be properly characterized (see Roswell, Dushoff, & Winfree, 2021 for a review). We compared taxonomic diversities of the habitats of the coastal and inland sites (not pooled) based on both number of individuals and sampled coverage and then compared taxonomic and trait-based diversities only on sample coverage. Taxonomic and trait-based rarefaction and extrapolations have been done using the iNEXT (Hsieh et al., 2016) and iNEXT.3D (Chao, 2021) packages.

As functional diversity indices are sensitive to missing trait data (Májeková et al., 2016), specimens with any missing trait value were excluded from the analysis. A total of 939 individuals were excluded from the dataset (814 individuals we could not identify to morphospecies, including 200 adults, and 125 specimens for which at least 4 traits were missing). The analyses were performed using R (R Development Core Team, 2021).

Results

A total of 1613 spiders were sampled, among which a total of 572 (35%) were adults and 1011 (64%) were juveniles. 940 spiders were collected at the coastal sites, and 673 at the inland sites (see details in Table 1).

Table 1: Overall presentation of the sampled spider assemblages over the four sites of French Guiana (CSG= Centre Spatial Guyannais) and four forest types (SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg).

		Total nb of individuals		Juveniles		Adults		Family nb	MS nb	Singletons nb	Doubletons nb	Nb of morphospecies with higher nb of individuals
		Nb	%	Nb	%	Nb	%					
CSG	SF	245		134	55%	109	44%	16	56	44	7	5
	TF	226		145	64%	80	35%	20	44	31	11	2
	WS	249		153	61%	95	38%	19	63	31	9	23
Laussat	SF	88		48	55%	36	41%	12	56	44	8	4
	TF	78		50	64%	27	35%	17	22	20	2	0
	WS	54		33	61%	21	39%	10	19	19	0	0
Nouragues	INS	31		19	61%	12	39%	13	5	2	3	0
	SF	117		66	56%	51	44%	18	22	17	4	1
Trinité	TF	204		152	75%	47	23%	20	22	19	1	2
	INS	49		38	78%	11	22%	14	9	7	2	0
	SF	141		88	62%	46	33%	20	36	32	2	2
	TF	131		85	65%	37	28%	19	28	27	1	0

Direct correlations between traits and between diversity metrics

Overall correlations between taxon- vs traits-diversities were high, whatever the metrics considered (yet the correlations tended to increase together from species richness, to Shannon and Simpson diversities, Figures 1 and 2). We will consequently focus on describing patterns of species richness for taxonomic diversity (TD) vs the four metrics of trait-based diversity (correlations between Shannon and trait-based diversity and Simpson and trait-based diversity will not be detailed in the text).

Single trait approach

Hunting guilds – The correlation between TD and FRic was moderate positive (Spearman correlation coefficient; $\rho = 0.45$, $P = 0.04$; Figure 1a). There was strong negative correlation between TD and FEve (Spearman correlation coefficient; $\rho = -0.91$, $P < 0.05$) and moderate negative correlation between TD and RaoQ (Spearman correlation coefficient; $\rho = -0.51$, $P = 0.01$).

Prosoma width – There was strong positive correlation between TD and FRic (Spearman correlation coefficient; $\rho = 0.67$, $P < 0.05$; Figure 1b). There was no significant correlation between TD and FEve (Spearman correlation coefficient; $\rho = -0.18$, $P = 0.43$) and RaoQ (Spearman correlation coefficient; $\rho = 0.40$, $P = 0.07$).

Tibia length – TD was strongly positively correlated to FRic (Spearman correlation coefficient; $\rho = 0.69$, $P < 0.05$; Figure 1c), and moderately to RaoQ (Spearman correlation coefficient; $\rho = 0.54$, $P < 0.05$). No significant correlation was found between TD and FEve (Spearman correlation coefficient; $\rho = -0.23$, $P = 0.31$).

Multi-trait approach

Hunting guilds and prosoma width – A moderate positive correlation was found between TD and FRic (Spearman correlation coefficient; $\rho = 0.59$, $P < 0.05$; Figure 2a). The correlation between TD and RaoQ was moderate negative (Spearman correlation coefficient; $\rho = -0.55$, $P < 0.05$). No significant correlation was found between TD and FEve (Spearman correlation coefficient; $\rho = 0.32$, $P = 0.15$) and FDiv (Spearman correlation coefficient; $\rho = -0.11$, $P = 0.64$).

Hunting guilds and tibia length – The correlation between TD and FDiv was moderate positive (Spearman correlation coefficient; $\rho = 0.50$, $P = 0.02$; Figure 2b). A strong negative correlation was found between TD and RaoQ (Spearman correlation coefficient; $\rho = -0.78$, $P < 0.05$). There was no significant correlation between TD and FRic (Spearman correlation coefficient; $\rho = 0.40$, $P = 0.07$) and FEve (Spearman correlation coefficient; $\rho = 0.39$, $P = 0.08$).

Prosoma width and tibia length – TD was strongly positively correlated to FRic (Spearman correlation coefficient; $\rho = 0.83$, $P < 0.05$; Figure 2c) and moderately correlated to RaoQ (Spearman correlation coefficient; $\rho = 0.55$, $P = 0.08$). There was not significant correlation between TD and FEve (Spearman correlation coefficient; $\rho = 0.10$, $P = 0.65$) and FDiv (Spearman correlation coefficient; $\rho = -0.007$, $P = 0.97$).

Hunting guilds, prosoma width and tibia length – A moderate positive correlation was found between TD and FRic (Spearman correlation coefficient; $\rho = 0.54$, $P < 0.05$; Figure 3). The correlation between TD and RaoQ was very strong negative (Spearman correlation coefficient; $\rho = -0.82$, $P < 0.05$). No significant correlation was found between TD and FEve (Spearman correlation coefficient; $\rho = 0.25$, $P = 0.26$) and FDiv (Spearman correlation coefficient; $\rho = 0.08$, $P = 0.73$).

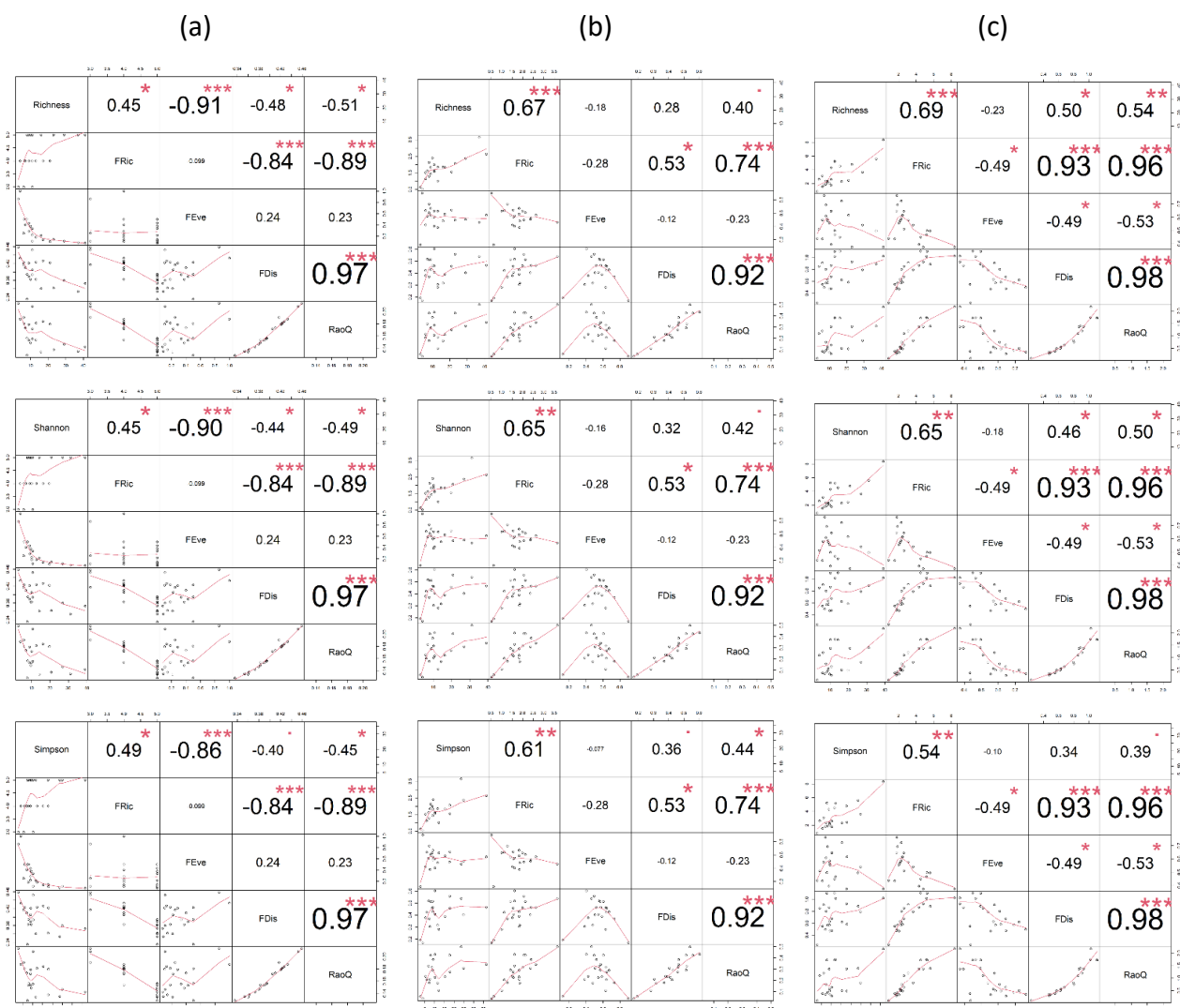


Figure 1: Correlations between TD (3 metrics) and trait diversity (4 metrics) depending on the trait considered for computing trait diversity (a: Hunting guilds, b: Prosoma width, c: Tibia length).

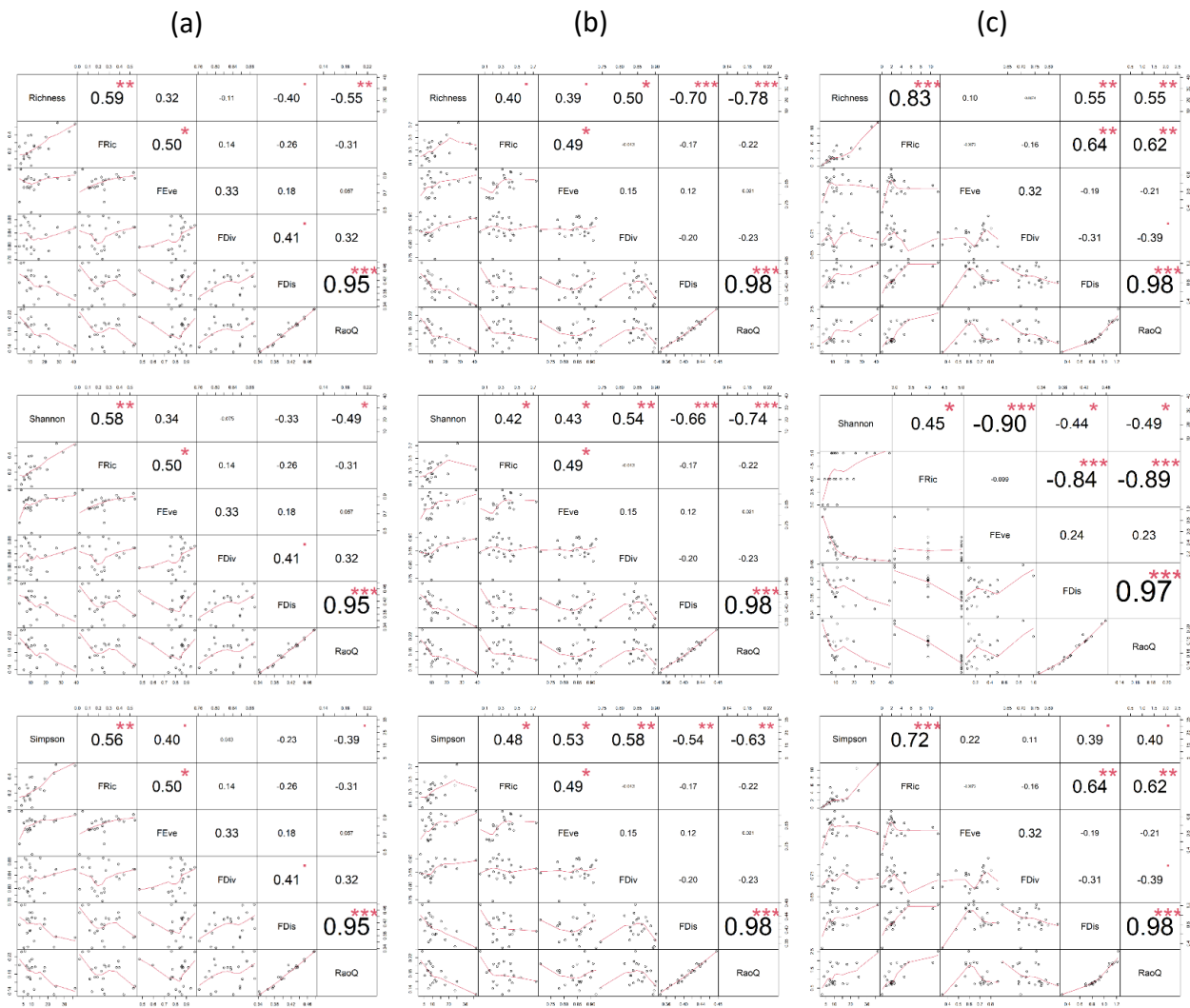


Figure 2: Correlations between TD (3 metrics) and trait diversity (4 metrics) depending on the combination trait considered for computing trait diversity (a: Hunting guilds and prosoma width, b: Hunting guilds and tibia length, c: Prosoma width and tibia length).

Comparison of patterns in taxonomic and trait-based diversity

Overall patterns of estimated taxonomic diversity were consistent between sites with similar environmental ranges (coastal vs. inland, Figure 4), with especially higher TD in WS forests vs SF forests and to a lesser extent compared to (coastal sites) and lower TD in Inselbergs forest as compared TD in TF and SF forests (the two latter were not significantly different in estimated TD, whatever q considered) (inland sites). Sites will consequently be mixed up in the subsequent results. Because of important variations of TD avoiding a proper comparison of the assemblages of the different habitats when estimations are based on the number of individuals, the subsequent comparisons of TD and trait-based diversity will be based on sample coverage.

Patterns of taxonomic diversity and influence of integrating juveniles

Whatever the metric considered and the stages integrated, forests on inselbergs had the lowest taxonomic diversity and forests on Terra Firme the highest (Figure 5). Integrating juveniles on top of adults did not influence TD patterns (see Figure 5a vs Figure 5c).

Patterns of trait-based diversity and influence of integrating juveniles

Whatever the metric considered and the stages integrated, forests on inselbergs had the lowest trait-based diversity and forests on Terra Firme the highest (Figure 6). Integrating juveniles on top of adults had little influence on trait-based diversity patterns (see Figure 6a vs Figure 6c).

Patterns of taxonomic vs. trait-based diversity

Patterns of taxonomic diversity vs trait-based diversity were finally very similar when compared for similar stages (see for adults: Figure 5a vs Figure 6a and for juveniles: Figure 5b vs. Figure 6b).

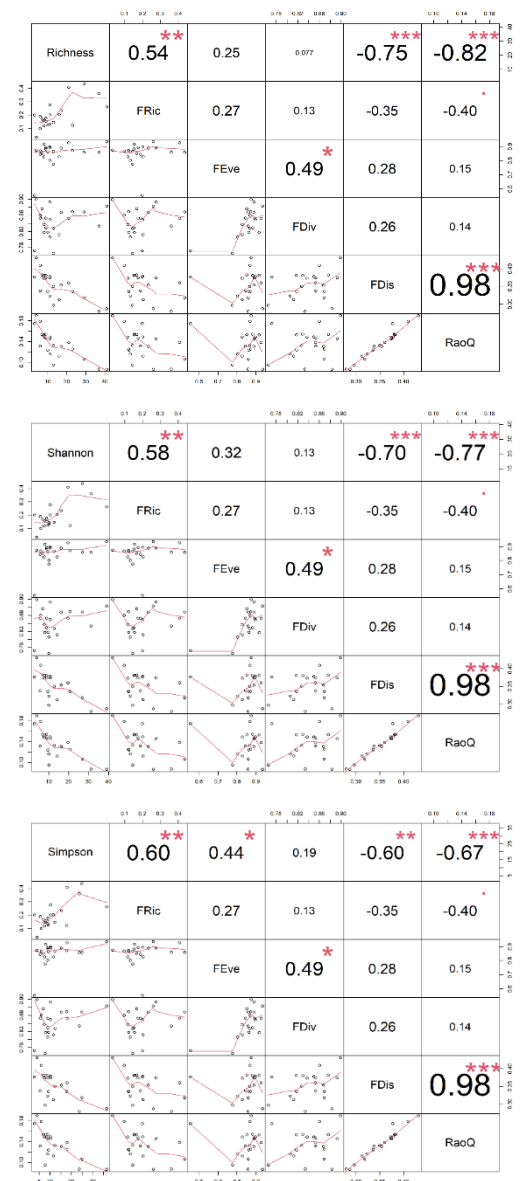


Figure 3: Correlations between TD (3 metrics) and trait diversity (4 metrics) for the combinaison of hunting guilds, prosoma width and tibia length.

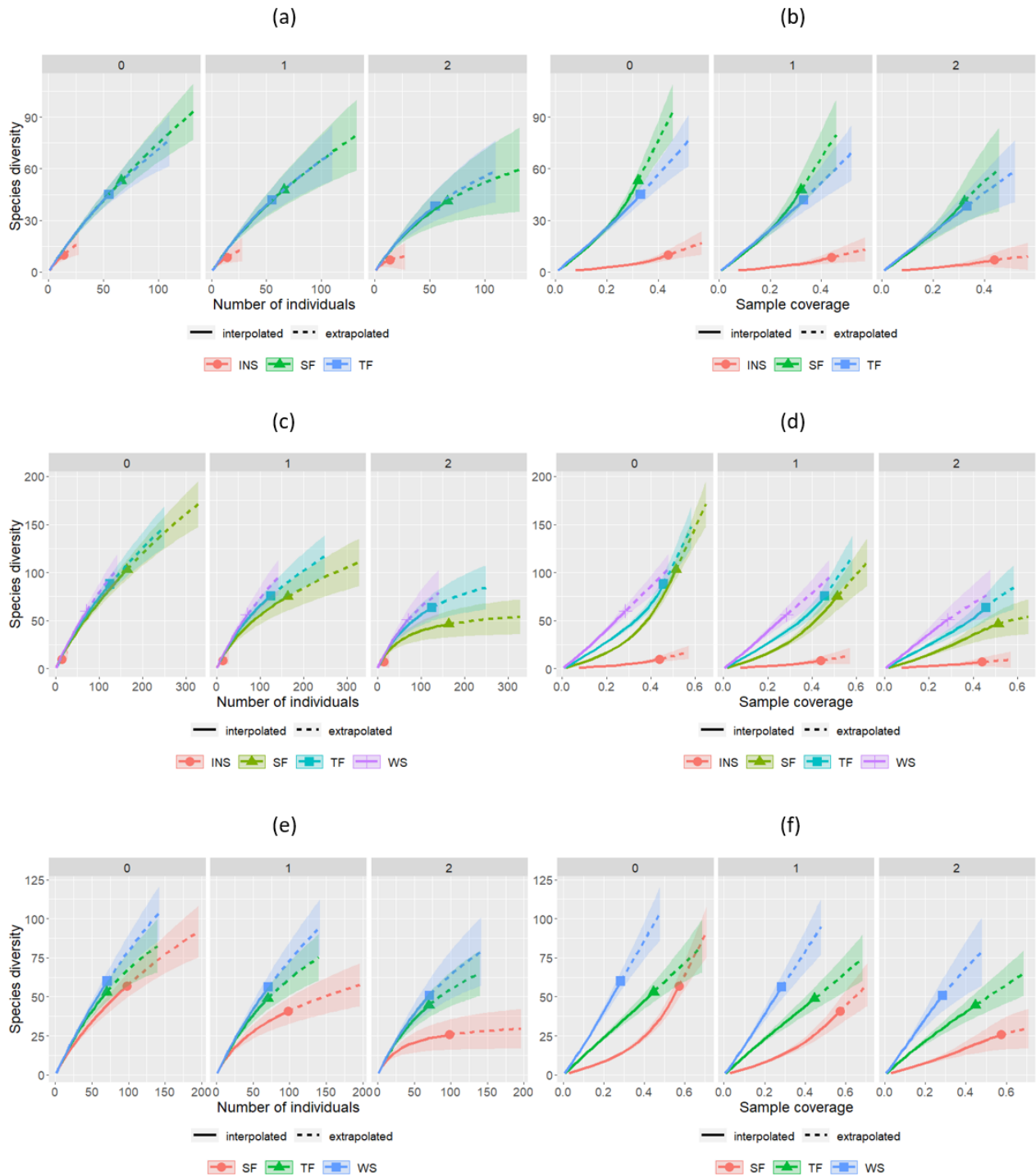


Figure 4: Estimated taxonomic diversity found between habitats based on number of individuals (left) or sample coverage (right) in coastal sites (a and b), inland sites (c and d), and all coastal and inland sites together (e and f). 0: taxonomic richness, 1: Shannon diversity, 2: Simpson diversity. Forest types: SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg.

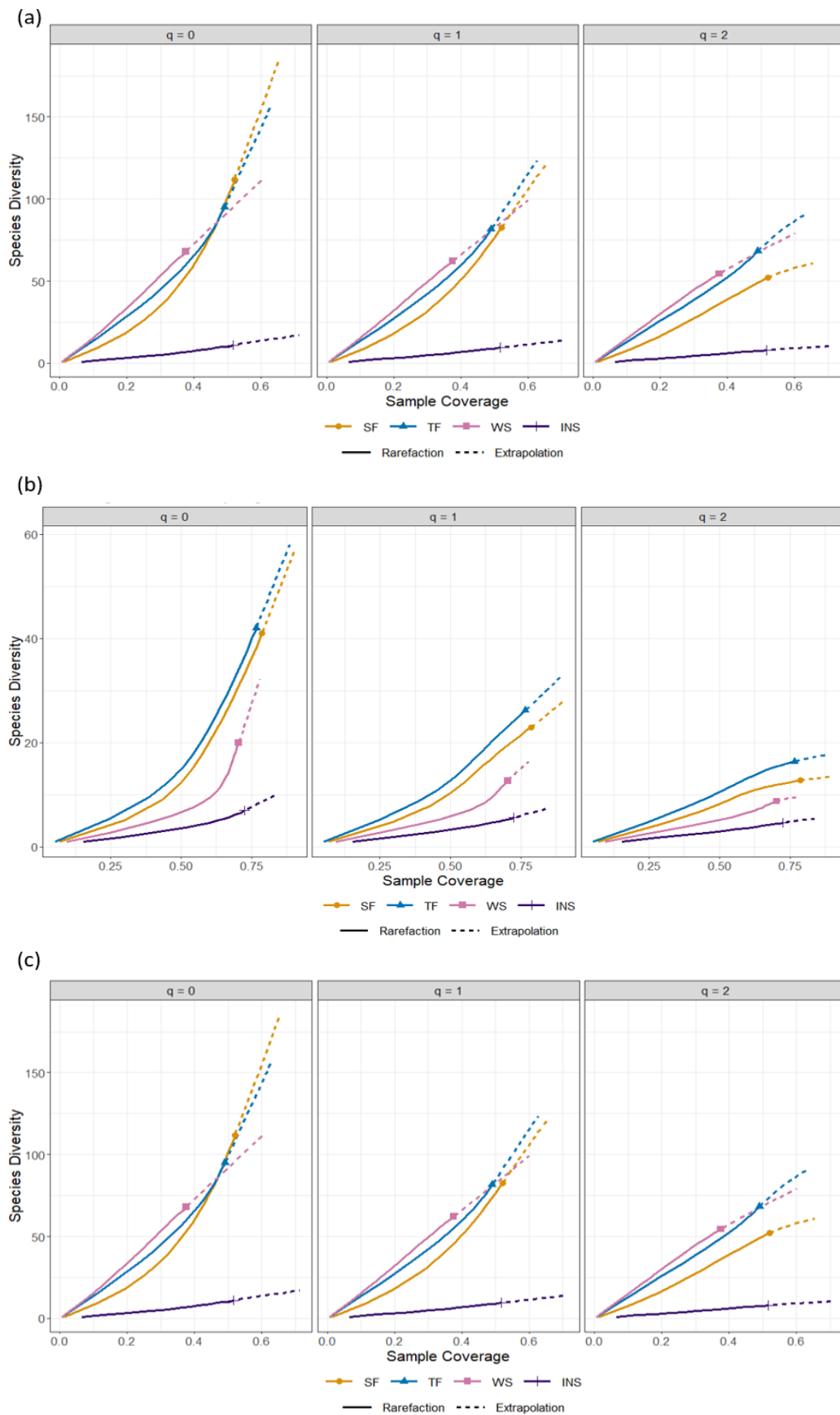


Figure 5: Estimated taxonomic diversity metrics in the 4 habitat types (SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg), considering adults only (a), juveniles only (b), or both (c).

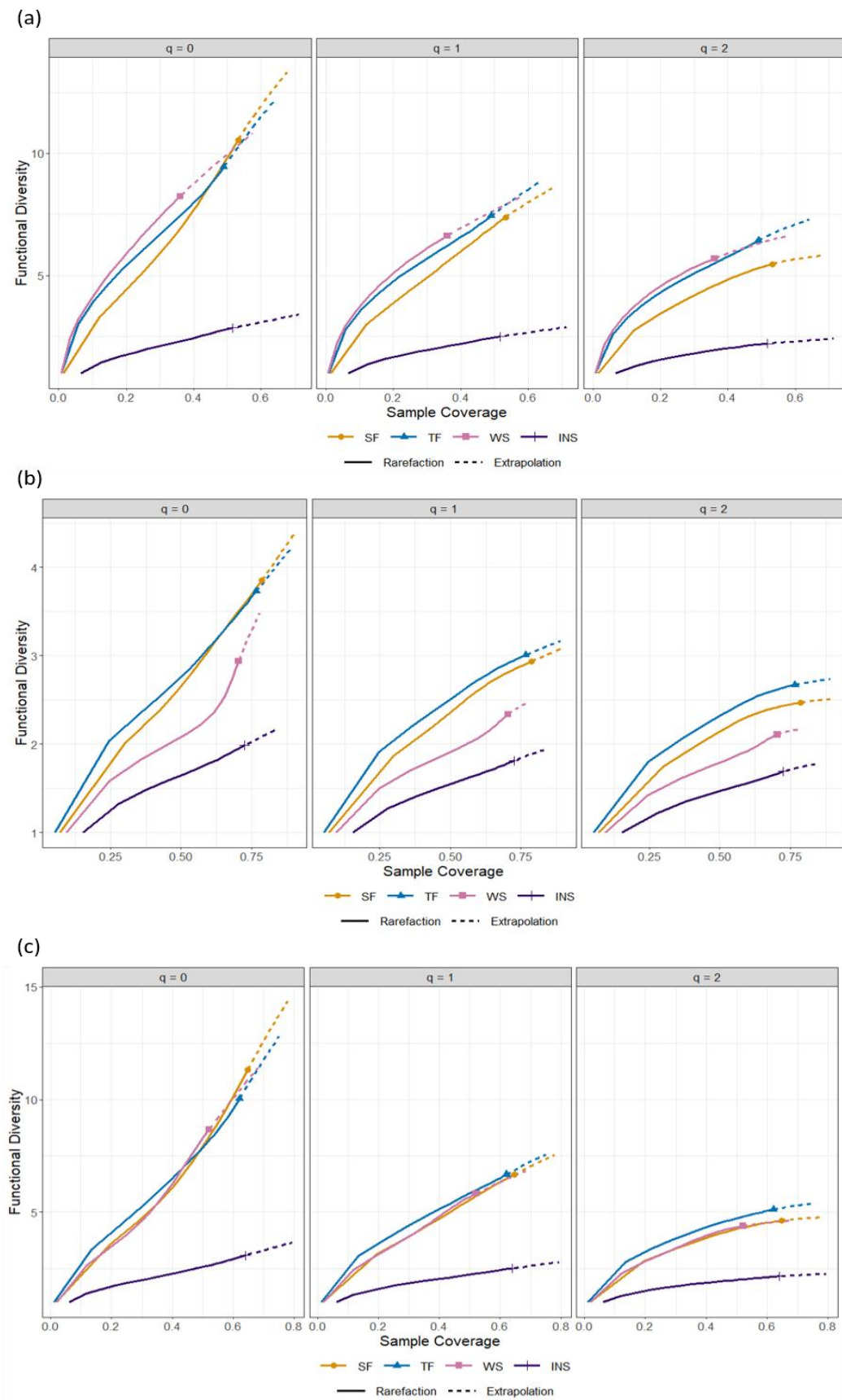


Figure 6 : Estimated trait diversity metrics in the 4 habitat types (SF=Seasonally Flooded, TF=Terra Firme, WS: White Sand, INS=Inselberg), considering adults only (a), juveniles only (b), or both (c).

Discussion

In this study, we investigated how taxon- and trait-based diversities vary across contrasted tropical forests habitats at broad geographical scales, and how several methodological impediments (number and nature of traits to be considered, integration of juveniles or not, q order) influenced the correlations of metrics (directly) and patterns (by comparison).

Overall taxon- and trait-based diversity metrics and patterns were highly correlated. Correlations between taxonomic and trait diversities are indeed supposed to increase with the level of environmental constraints (for plants: Cadotte et al., 2019), and one would expect lowered correlations in tropical habitats (see also Privet & Pétillon, 2020 for spiders). Our results also show a significant influence of forest type on both taxonomic and trait diversity patterns, probably revealing strong environmental filtering (see Ridet et al., 2021 for another example in, temperate, spiders; see also Fichaux et al., 2019 for an example on hyperdiverse taxa of arthropods in neotropical forests). The range of forests sampled in this study comprised contrasting soil, plant community structure and composition (Baraloto et al., 2007, 2011; Fine et al., 2010; Wittmann et al., 2011; Fortunel et al., 2014) driving differences in potential prey environments and shelters for arthropods (Price, 2002). A recent study, conducted in the same forests, has found that taxonomic and functional composition of arthropods assemblages (including Coleoptera, Lepidoptera, Hemiptera, Hymenoptera and Orthoptera but only a family of spiders) show a strong turnover among habitats (Lamarre et al., 2016). However, there are no differences in herbivory rate among these habitats (Lamarre et al., 2012) despite the plant defense theory (Janzen, 1974; Coley et al., 1985). The plant defense theory predicts fewer resources allocated in anti-herbivory defense in high-resource plant communities, such as terra firme and seasonally flooded forest, compared to low-resource plant communities, such as white sand forest and inselberg forests (Baraloto et al., 2013).

One potential explanation for the lack of differences in herbivory rate may be the strength of the third trophic level, such as predators (spiders) and parasitoids, that regulates herbivore populations (Van Bael et al., 2003). This hypothesis, if proved, does not however explain the case of white sands forests which are low-resource plant communities with no different herbivory rate (Lamarre et al., 2012) but the lower abundances of arthropods (Lamarre et al., 2016) and intriguingly the highest taxonomic and functional diversities in spiders found in our study. White sand forests are characterized by specific vegetation (Medina et al., 1990; Fine et al., 2010) and unique assemblage of arthropods (including white-sand habitat specialists such as Delphacidae and Fulgoridae (Hemiptera), Lamarre et al., (2016)) but are also located within the terra firme and seasonally forests (Fine & Bruna, 2016). It would thus be interesting to investigate white-sand forests spiders taxa composition and diet to see if they are similar to the one of the surrounding forests with the addition of spiders feeding preferentially on white-sand arthropods specialists.

Conversely, the lowest taxonomic and trait diversities were found on inselbergs, which is consistent with other studies on neotropical spiders (see e.g. Lalagüe et al. submitted and Privet et al., (2018)). Several factors were advocated to explain such a pattern, and these included harsh microclimatic conditions, thinner soil, and species-poorer vegetation (as compared with lowland conditions). The quite low taxonomic and functional diversity in seasonally flooded forests, especially visible when adults of spiders were considered (with juveniles or not), might finally be explained by the removal of litter and the absence of vegetation succession due to floods, which in turn affect spider assemblages, reducing both taxonomic and functional diversities (see e.g. Uetz, 1979 and Döbel et al., 1990, respectively).

Correlation between taxonomic and trait diversity is also expected to increase with the number of traits used (see for plants: Tucker et al., 2018). While several traits were highly correlated to each other, hunting guilds drove most of the trait diversity patterns (results not presented here but see Figure S1 in supplementary material), highlighting the importance of this trait in spider community ecology. Yet this trait needs to be carefully used because they might differ among species within one family (Dias et al., 2009) and probably within individuals of a given species (Suter & Benson, 2014). The trait composition of spiders assemblages will be determined and compared among the different habitats in the near future. Patterns of body size, if detected, could inform us on the size of the ecological niche of species (Novotný et al., 2006). Smaller species are expected in cooler environments, e.g. at high latitudes or altitudes (Entling et al. 2007), thus it could be that smaller individuals can be found on the inselbergs. Conversely, if no differences in body size are among habitats, that could be because the effects of elevation are lesser under tropical conditions (mainly because of a reduced temperature range: Overgaard et al., 2011). Another explanation could be that the effects of altitude on spider size (i.e. an increase in spider size: see e.g. Ameline et al., (2018)) might be balanced by soil succession and the resulting reduced prey availability (see Kounda-Kiki et al., 2004). Regarding other biometric traits we measured, longer legs were proved to increase speed on steep ground (Prenter et al., 2012), while proportionally shorter legs in flooded habitats were reported for one species of Ctenidae, some wandering spiders of tropical forests (Pétillon et al., 2018). Last, one should stress that size constraints on legs differ between web-building and cursorial spiders (Moya-Laraño et al., 2008). These hypotheses should be tested soon by looking at in-detail trait variations among habitat types.

While our results suggest important environmental filtering, even in tropical forests, the relative importance of deterministic vs neutral processes remains to be tested in the assembly rule of tropical forest spiders. Barcoding using several sequences could be used in complement to our current approaches to 1) challenge morphological segregation (see Courtial et al. in prep, Appendix 3 of the thesis) and be used to assess the phylogenetic diversity (see Dolson et al., 2020). The importance of juveniles could be then more important than what we observed when they are integrated into molecular approaches (Domènech et al., 2021). Environmental variables describing climate, soil and forest structure are available for these habitats (for complete details, see Baraloto et al., 2011). They were previously used in order

to define the environmental conditions of each studied plot (Lamarre et al., 2016) and will be used in the future to investigate the relationships between traits and environmental conditions as well as spider taxonomic and trait assemblages. The influence of species and traits in composition turn-over (patterns of β -diversity using Hill numbers) should also be investigated in the close future. Differences in environmental drivers are indeed expected between taxonomic and trait diversity, with complementary responses to abiotic gradients (see Wong et al., 2019 for a recent, general, review on arthropods). If the nestedness of beta taxonomic diversity is reported to increase when the number of species decreases (e.g. Hacala et al., 2020), this remains unexplored for beta trait (functional) diversity. Our study finally calls for better standardization of metrics, in terms of estimation methods and type of metrics (with a little influence of q order, except for increasing correlations between taxonomic and trait diversity metrics), but also for more actually-measured traits in arthropod community ecology.

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Supplementary Materials

Comparison of trait diversity with and without hunting guilds

Adults, juveniles and adults+juveniles trait diversity excluding hunting guilds, compared with the above plots including hunting guilds, reveal that hunting guilds is an influential traits (note the Y-scales are different, although patterns are generally similar).

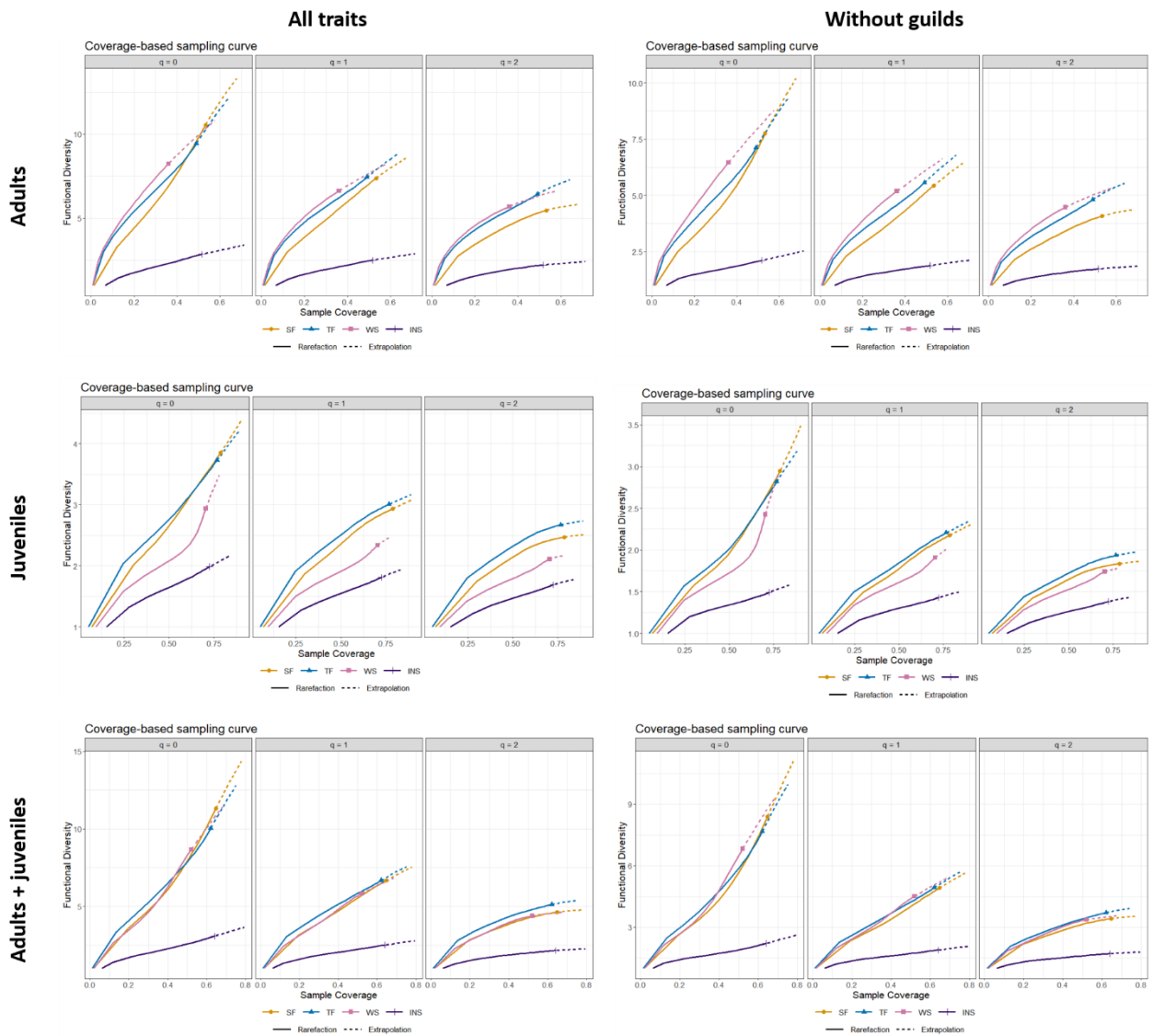


Figure S1: Patterns of trait diversities between habitats compared when all traits are taken into account (left column) and when hunting guilds are excluded (right column). Patterns for adults (first column), juveniles (second column) and both (third column) are shown.

PART III : DÉCRIRE ET COMPRENDRE LA DIVERSITÉ DES ARAIGNÉES TROPICALES PAR L'APPROCHE PHYLOGÉNÉTIQUE : LE CAS DES ARAIGNÉES LOUPS D'HAWAÏ

CHAPITRE.5

Les relations phylogénétiques entre les araignées-loups hawaïennes suggèrent une radiation récente due à l'adaptation à différents environnements.

Phylogenetic relationships among Hawaiian wolf spiders suggest recent radiation driven by the adaptation to different environments

Kaïna Privet, Henrik Krehenwinkel, Rosemary Gillespie and Julien Pétillon

This article is in preparation

Abstract

Understanding the origins of diversity patterns is a major challenge in ecology and adaptive radiation has been proposed as its main contributor. We used a system of wolf spiders distributed across different ecological conditions over islands of different ages in the Hawaiian archipelago to investigate the pattern of phylogenetic relationships among taxa across islands as well as the role of habitat and altitude specialization vs. dispersal. We developed a detailed, phylogenetic framework to determine boundaries and phylogenetic relationships between taxa. To do so we gathered the complete collection of wolf spiders from the Hawaiian archipelago so far and investigated their phylogenetic relationships using a set of molecular markers and a high throughput next-generation sequencing approach to obtain data representative at multiple time-slices within the phylogeny. The preliminary results show single-locus phylogenetic trees of low resolution with incongruencies between loci. Despite this, these trees support lineages occurring on single or multiples islands. They also support an independent lineage of cave spiders including few surface relatives suggesting that adaptation to cave environment is evolutionarily labile for these spiders. Among surface spiders, no congruent pattern of altitude-related speciation was found but further analyzes are needed to better capture the role of altitude in Hawaiian wolf spider speciation.

Keywords: ecological divergence, Hawai'i, Lycosidae, cave, introgression, phylogeography.

Introduction

Understanding the origins of diversity patterns is a major challenge in ecology. Current diversity is the product of ecological and evolutionary processes and their interactions. One process, **adaptive radiation**, has been proposed as the major contributor to global diversity (Simpson 1953, Schluter 2000). Adaptive radiation is the process by which organisms rapidly diversify from an ancestral species into a multitude of different new ecological forms (Gillespie *et al.* 2001). Adaptive radiation requires ecological differentiation coupled with reproductive isolation to allow speciation (Rundell & Price 2009). Adaptive radiation is thus acting at the intersection between ecology and evolution. Divergent natural selection arising from environmental or niche differences can lead to ecological divergence and speciation (called “ecological speciation”) and is thought to play a major role in driving adaptive radiation (Schluter 2000, Rundle & Nosil 2005, Nosil 2012). **Ecological speciation** has been well illustrated in many examples of recent adaptation of incipient species (e.g. Cichlid fishes and Asteraceae, respectively, Meier *et al.* 2018, Knope *et al.* 2020). However, the extent to which divergence into different habitats can lead to adaptive radiation is still unclear (Gillespie *et al.* 2020).

Islands, and in particular remote oceanic hotspot islands with a geological chronology, have been proposed as a system sufficiently simple to master at least some of the complexity, history, geography, and evolutionary adaptation required to untangle the origins of biodiversity in the context of adaptive radiation (Gillespie 2016). The **islands of Hawaii** are notably an unparalleled scientific laboratory for studying ecological and evolutionary processes at the origin of diversity due to their particular characteristics (Carson 1982, Baldwin & Sanderson 1998, Lerner *et al.* 2011, Brewer *et al.* 2015, Gillespie 2016, Gillespie *et al.* 2018). Indeed, the Hawaiian archipelago shows (i) extreme isolation, which results in the reproductive isolation of the colonists and can lead to speciation. Moreover, the Hawaiian archipelago consists of (ii) a series of islands that provides a replicated system for examining within-islands patterns of species formation across similar ranges of environmental extremes, and (iii) a chronological arrangement of the islands from Kauai (oldest) to Hawai’i (youngest) (Figure 1) that allows the examination of species formation within an identifiable chronological framework (Carson & Clague 1995). Finally, the Hawaiian archipelago also has (iv) a tremendous topographical range, a tropical position, a great range of climatic zones (Neall & Trewick 2008), and consequent environmental diversity that provides a huge ecological spectrum for species differentiation. Due to their age, the older islands of the Hawaiian archipelago have undergone erosion. However, the youngest island of Hawaii, is currently located over the hot spot and still has active volcanoes (the last eruption started on September 29, 2021), making the Hawaiian archipelago the group of islands that reaches the greatest altitude with the twin peaks of Mauna Kea volcano at 4207 m and Mauna Loa volcano at 4169 m (Figure 2).

Spiders are particularly suitable organisms to study patterns of diversification at the intersection between ecology and evolution because their ecology is readily apparent through their very tight habitat affinities (Foelix 2010) and their observable hunting behaviors. On the islands of Hawaii, the **wolf spiders (Lycosidae)** are found from low to high elevations, on coastal sites, wet forests, lava flows, summit deserts, and likewise in lava caves (Keyserling 1890, Simon 1900, Gertsch 1973, Howarth 1983, 1987b, Duman & Montgomery 1991). Therefore, they are one of the spider families whose ecological range includes the most contrasting physical environments in the Hawaiian archipelago (Howarth & Montgomery, 1980). Across these well-defined habitats, Hawaiian wolf spiders show marked morphological and lifestyle differences: there are web-spinning wolf spiders in forests (Simon 1900) and ground-dwelling wolf spiders on surface lava flows (Howarth & Montgomery 1980). In lava caves, wolf spiders show reduction or loss of eyes and body pigments (Howarth 1972, Gertsch 1973), along with other attributes to subterranean existence, including low reproductive rates, a reduced number of offspring, and long periods to maturity (Hadley *et al.* 1981, Howarth 1993). These differences suggest the possibility that Hawaiian wolf spiders differentiated across habitats unlike most other endemic spider taxa in Hawaii that have largely diversified within the same environment (wet forest) (Hiller *et al.* 2019), such as *Tetragnatha* (Tetragnathidae)

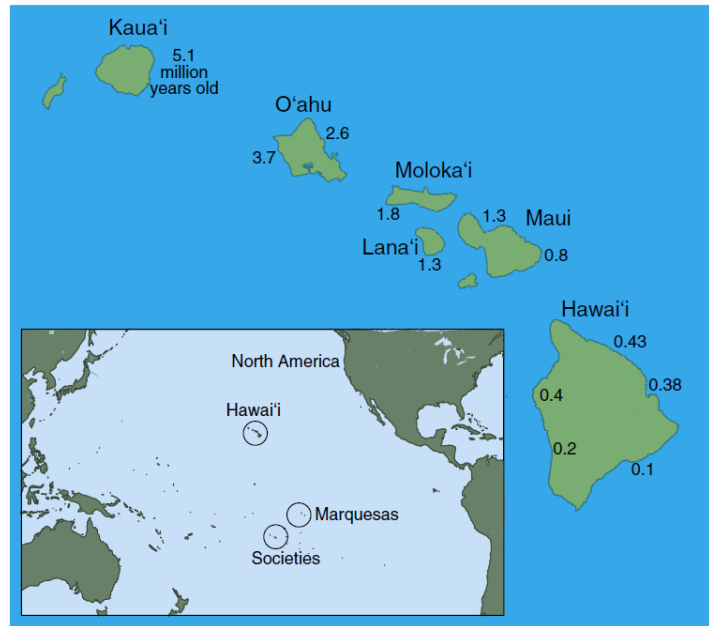


Figure 7: The Hawaiian archipelago chronosequence. The numbers indicate volcano geological ages, in millions of years. The still-growing island of Hawai'i is the youngest (reproduced from Gillespie, 2005).

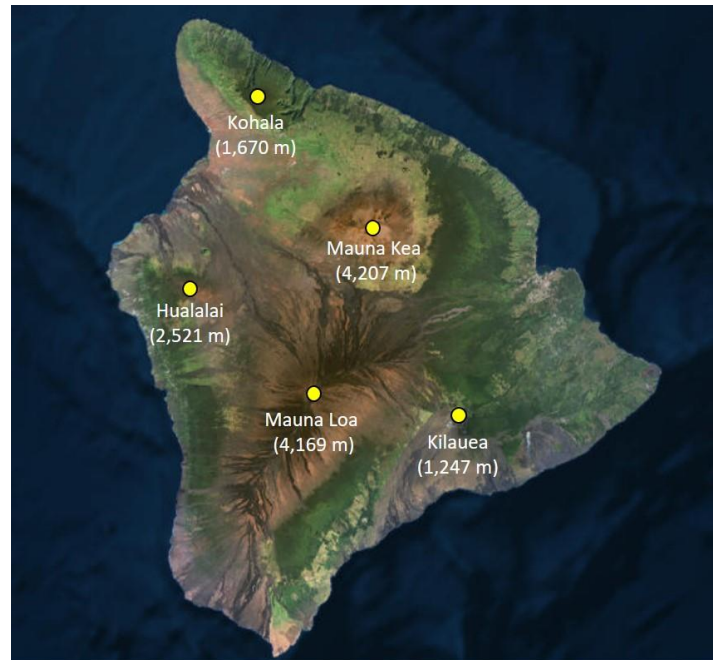


Figure 8: Map of the island of Hawaii mentioning the five volcanoes and their elevation.

These differences suggest the possibility that Hawaiian wolf spiders differentiated across habitats unlike most other endemic spider taxa in Hawaii that have largely diversified within the same environment (wet forest) (Hiller *et al.* 2019), such as *Tetragnatha* (Tetragnathidae)

(Blackledge & Gillespie 2004, Blackledge *et al.* 2009), *Ariamnes* (Theridiidae) (Gillespie *et al.* 2018), *Mecaphesa* (Thomisidae) (Garb & Gillespie 2009) and *Havaika* (Salticidae) (Arnedo & Gillespie 2006).

This study aims to address the hypothesis that population divergence and species formation in Hawaiian Lycosidae are associated with adaptation to different environments in allopatry.

In the Hawaiian islands, 18 species of wolf spiders in 11 genera (see the list in Table 1) (Suman 1964, Gillespie *et al.* 1998, Nishida 2000) are currently named. Among those, 11 are thought to be endemic (Suman 1964, see Table 1). The endemic species belong to two subfamilies and seven genera: Lycosinae (*Hogna*, *Trochosa*, *Alopecosa*, *Adelocosa*, *Lycosa*) and Artoriinae (*Lycosella*, *Syroloma*). The Lycosinae subfamily has a worldwide distribution while Artoriinae is known from Australasian, Oriental, Pacific regions (Framenau 2007) and South America (Piacentini & Ramírez 2019). In the Hawaiian islands, the Lycosinae subfamily are ground-, lava-, and cave-dwelling spiders, while Artoriinae are vegetation web-spinning spiders. These two subfamilies suggest that there have been at least two colonization events and sources at the origin of the Hawaiian wolf spider fauna.

However, assignments to genus and species may have little validity for these Hawaiian wolf spiders. Wolf spiders represent relatively recent radiation of arachnids (Jocqué & Alderweireldt 2005, Garrison *et al.* 2016, Wheeler *et al.* 2017) with a strong morphological conservatism which has caused enormous confusion in their systematics (e.g. paraphyletic and polyphyletic genera) due to the lack of useful characters to define and separate genera and species (Vink *et al.* 2002, Jocqué & Alderweireldt 2005). Their morphological conservatism seems even more prominent on the Hawaiian archipelago and we are lacking characters to separate species (Framenau, pers. comm.; Pétilon, pers. comm.). Within the Lycosinae subfamily, it has been suggested that all species belong to the genus *Hogna* and they are more species than what is currently described (Framenau, pers. comm.). Thus, **the current species designations are questionable** but no taxonomic revision has been performed to date. Moreover, **knowledge about the described species is limited** as we have incomplete information on the natural history and the distribution of the described species. **Consequently, the genetic approach seems essential to better describe and understand their diversity and its origin.**

Using this system of wolf spiders distributed across different environments over islands of different ages in the Hawaiian archipelago, we developed a detailed, phylogenetic framework to **determine species boundaries and phylogenetic relationships between taxa.** We aim at answering the questions developed hereafter.

Table 2: List of the named wolf spider species from the Hawaiian archipelago known to date. Distributions are given according to the World Spider Catalog (2021), species descriptions, Hawaiian checklist (Nishida 2000), and arachnologist databases (Volker Framenau, pers. comm.). See Figure S1 for a map of the distribution of the endemic species in the current state of knowledge.

Subfamily	Genera	Species	Distributions	Status in Hawaii
Lycosinae	Adelocosa	<i>Adelocosa anops</i> Gertsch, 1973	Hawaii (Kauai is.)	Endemic
	Alopecosa	<i>Alopecosa oahuensis</i> (Keyserling, 1890)	Hawaii (Oahu and Hawaii is.)	Endemic
	Arctosa	<i>Arctosa aliusmodi</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
	Hogna	<i>Hogna bruta</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
		<i>Hogna crispipes</i> (L. Koch, 1877)	Australia (mainland, Norfolk Is.), New Guinea, Vanuatu, Polynesia, New	Introduced (all islands)
		<i>Hogna hawaiiensis</i> (Simon, 1899)	Hawaii (Oahu, Maui and Hawaii is.)	Endemic
	Lycosa	<i>Hogna likelikeae</i> (Simon, 1900)	Hawaii (Kauai is.)	Endemic
		<i>Lycosa howarthi</i> Gertsch, 1973	Hawaii (Hawaii is.)	Endemic
		<i>Lycosa perkinsi</i> Simon, 1904	Hawaii (Oahu is.)	Endemic
	Schizocosa	<i>Schizocosa vulpecula</i> (L. Koch, 1865)	Wallis is.	Introduced (Maui is., Oahu is.)
	Trochosa	<i>Trochosa kalukanai</i> (Simon, 1900)	Hawaii (Kauai is.)	Endemic
	Vesubia	<i>Vesubia caduca</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
Artoriinae	Anoteropsis	<i>Anoteropsis virgata</i> (Karsch, 1880)	Polynesia	Introduced (Maui is.)
	Lycosella	<i>Lycosella annulata</i> Simon, 1900	Hawaii (Oahu is.)	Endemic
		<i>Lycosella spinipes</i> Simon, 1900	Hawaii (Kauai and Hawaii is.)	Endemic
	Syroloma	<i>Syroloma major</i> Simon, 1900	Hawaii (Kauai, Oahu, Maui and Hawaii is.)	Endemic
		<i>Syroloma minor</i> Simon, 1900	Hawaii (Kauai, Molokai, Maui and Hawaii is.)	Endemic

Question 1: what are the phylogenetic relationships between wolf spiders found on different islands?

Based on preliminary data, it appears that: (i) members of the subfamily Lycosinae are likely all within the genus *Hogna*, and are morphologically conserve at the surface, (ii) members of the

subfamily occurs at different elevations at the surface of all the main islands, and down to caves on two islands, we suggest that:

Hypotheses: Hawaiian wolf spiders “morphological conservatism” might reflect the absence of differentiation of surface spiders, related to a recent radiation or gene flow occurring between diverging lineages found on different islands and among islands on different elevations.

Question 2: What are the phylogenetic relationships between surface spiders found at different elevations? Is there an altitudinal pattern of phylogenetic relationships? The case of the island of Hawaii

The surface members of the Lycosinae (in contrast to those in caves) are found from low to high elevations. Investigations conducted prior to this thesis, by Julien Pétillon (unpublished), on wolf spiders found all along the slope of the Mauna Kea volcano (above 1000m to the summit) from the island of Hawaii (Figure 2), concluded that these wolf spiders seem morphologically very similar although showing confusing genitalic diversity for a single species. It was thus not possible to determine if they were different species or populations of the same species. These wolf spiders encounter very different living conditions. The wolf spiders found at the summit of the Mauna Kea volcano (>4000 m) live in an alpine stone desert covered by snow for part of the year (high altitude aeolian system) (Howarth & Montgomery 1980, Englund *et al.* 1999). This alpine desert consists mainly of a mix of unvegetated lava rock and semi-vegetated lava flows, covered by alpine tundra (Hawaiian tropical high shrublands). The precipitation is low and the temperatures are extremes with warm days and cold nights (Howarth 1987b). The wolf spiders hide in cracks and under rocks during the day and only venture onto the surface at night or when suitable prey appears (Howarth 1987b). Duman & Montgomery (1991) highlighted that one of these species (referred to as *Lycosa sp.*) is not freeze tolerant but survives by avoiding low temperatures through high mobility to quickly move into thermally buffered microhabitats. Other wolf spiders found along the slope of the volcano live on lava flows, one of the most inhospitable environments on earth (neogeoaeolian system, Howarth 1979). There the daily surface temperature fluctuations often approach 50°C and the rain either percolates into the porous rock or evaporates to render it very xeric (Howarth 1987b). These lava flow are from different ages, and left intact some “islands” of vegetation are called “kipuka”, from which wolf spiders are surprisingly absent (Vandergast & Gillespie 2004, Pétillon *et al.* 2020).

Hypotheses: consequently, we suggest that the living conditions on these ecosystems are harsh and differs between summit (Aeolian system) and slope (Neogeoaeolian system). Therefore, there could be two ecotypes (species adapted to specific environmental conditions): the first living in the alpine desert of the summit, the second living on lava flows on the slope of the volcano.

Question 3: What are the relationships among cave wolf spiders and between cave- and surface wolf spiders?

Among the endemic wolf spiders of the islands of Hawaii, two species (*Adelocosa anops* and *Lycosa howarthi*) are troglobitic and have adapted to cave life through eye and pigment modification, as well as physiological changes (Hadley *et al.* 1981). With another species found in French Polynesia (*Nukuhiva adamsoni*) (Framenau & Lehtinen 2015), these are the only known representatives of cave adaptation in wolf spiders globally (Mammola & Isaia 2017). A first species, *Adelocosa anops* Gertsch, 1973, is found on the oldest high island (Kauai) and has undergone a complete loss of eyes (Gertsch 1973) (Figure 3). A second species, *Lycosa howarthi* Gertsch, 1973, is found on the youngest island (Hawaii) and has only undergone a reduction of its eyes (Figure 3) (Gertsch 1973, Hadley *et al.* 1981, Howarth 1987a). This species is found in cave systems of different ages (Table 3).

Hypotheses: Considering that the islands of Kauai and Hawaii have never been connected, we suggest that the two troglobitic species have evolved independently from surface relatives. We test the hypothesis considering that the difference in eye loss and islands between these two species could be related to (1) independent colonization of caves from surface relatives (*L. likeliikeae* on Kauai; *H. hawaiiensis* on the island of Hawaii), and (2) the older age of Kauai (5 my) compared to Hawaii (0.5 my), resulting in a longer time to adapt to cave life (Howarth 1993, Framenau & Lehtinen 2015). On the island of Hawaii, *L. howarthi* is found in cave systems that of different ages. We thus suggest that the species colonized the caves multiple times, allowing the assessment of divergence replicated on the same landscape but at different times.

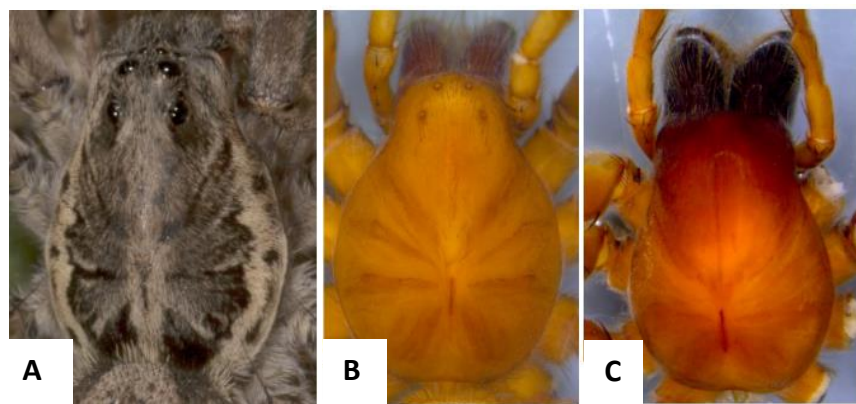


Figure 3: A: surface-dwelling Hawaiian wolf spider (*Hogna crispipes*); B: cave-dwelling wolf spider with reduced eyes (*Lycosa howarthi*) only known from the youngest island of the archipelago (Hawaii); C: cave-dwelling wolf spider with no eyes (*Adelocosa anops*) known from the oldest island of the archipelago (Kauai). (Images from Framenau and Lehtinen, 2015).

We tested these hypotheses by collecting spiders from the main islands of the archipelago, from cave and surface. We then studied their phylogenetic relationships using a set of nuclear and mitochondrial markers and high throughput sequencing approach to obtain data representative at multiple time-slices within the phylogeny. We present here preliminary results obtained on their phylogeny.

Materials and methods

Taxonomic sampling

For this study, we gathered a total of 217 spiders from 9 islands (see Tables 2 and 3 for details on the collected samples and the caves but see Table S1 in supplementary data for a complete list). Some of these samples were from field trips conducted on the islands of Molokai and Hawaii between 2016 and 2017. These specimens were kept in 96% or 100% ethanol at -20°C before extraction. Other field expeditions were planned during this Ph.D. to complete the sampling for most of the main Hawaiian Islands but were canceled due to the Covid-19 pandemic. The other part is museum specimens, mostly not identified to species, that were collected from 1931 to 2017 and provided by the Bernice Pauahi Bishop Museum (Honolulu, USA), Muséum National d'Histoire Naturelle (Paris, France), the Queensland Museum (Queensland, Australia), the Essig Museum of Entomology (Berkeley, USA), the Musée des Confluences (Lyon, France) and personal collections (Rosemary Gillespie, Jesse Eiben, Megan Porter, Natalie Graham). Most of these specimens were kept in 70% ethanol at room temperature since their collection.

Spiders identified as *Hogna crispipes* (introduced) are included to ascertain their phylogenetic assignments, as well as spiders belonging to the other subfamily known from the Hawaiian Islands, Artoriinae. The originally described species of Artoriinae have not been recorded during our field trips and we consequently used Museum material. Moreover, we included specimens of *Hogna radiata*, the European type species of the genus *Hogna* to test the taxonomic placement of Hawaiian *Hogna*, and a specimen of *Bradystichus crispatus* (Pisauridae) as the outgroup.

Table 2: Origin of the wolf spiders studied according to the island, volcanoes, and elevations they were collected in. Information about the date of collection is given.

	Islands (from oldest to youngest)	Number of specimens	Volcanoes/elevation (maximum elevation on the island)	Date of collection	
Northwestern Hawaiian islands	Laysan	3	-	1959-1987	
	Necker	2	-	1982	
	Nihoa	2	0m	2015-2016	
Main Hawaiian islands	Kauai	20 including	16	Up to 1158m (max 1598m)	1963-2016
			4	Caves – Koloa caves (3), Kiahuna (1)	1971-1979
	Oahu	15		Up to 700m (max 1220m)	1933-2015
	Molokai	21		0-300m (max 1512m)	2016
	Lanai	1		457m (max 1026m)	1973
	Maui	20		0-3000m (max 3055m)	1975-2016
	Hawai'i	133 including	1	Hualalai volcano – 1310 m (max 2521m)	1972
			55	Mauna Kea volcano – up to 4168 (max 4207m)	1992-2018
30			Mauna Loa volcano – up to 4053m (max 4169m)	1971-2016	
27			Kilauea volcano – up to 1247m (max 1247m)	1971-2016	
		20	Caves – Kaumana cave system (1), Happy hobbit cave system (1), Kipuka Kanohina cave system (18)	No date, 2016, 2018	

Table 3: Island, volcano, age and altitudes of the sampled caves.

Island	Volcano	Cave system	Cave (section)	Age* in years	Elevation in m**
Kauai		Koloa Cave 2	Kiahuna	150,000-500,000	0
Hawai'i	Mauna Loa	Kaumana	Kaumana cave	140 (1881 flow)	300
	Mauna Loa	Keokeo	Happy Hobbit	1,500-3,000	550-750
	Kīlauea	-	Ainahou cave	550-600 (Aila'au Flow)	920
	Kīlauea	Kazamura	Kazumura cave	550-600 (Aila'au Flow)	410
	Mauna Loa	Kipuka Kanohina	Kula kai	1,500-3,000	900
			Akea ka Mai	750-1,500	200-450
			Cordwinder Cave	750-1,500	200-450
			Eli's Cave	750-1,500	200-450
			Maelstrom	750-1,500	200-450
			Sea reef	200-1,000	1,150-1,400
		Xanadu	750-1,500	100	

* lave flows, according to Barton & Charlesworth 1984, Templeton 2008, Bosted *et al.* 2013, Aue 2014)
 ** at cave entrance, rounded

Selection of molecular markers of interest

Choosing markers to study the Hawaiian wolf spider radiation was a compromise of several criteria including (1) the need to study multiple time-scales to unravel the diversification and colonization patterns, (2) the fact that most of the samples are museum samples with degraded DNA, (3) the relatively recent age of the family, (4) the absence of a broad-scale phylogeny of the family, (5) the presence of paralogous copies of nuclear genes (Murphy *et al.* 2006) and (6) the mitonuclear discordance in wolf spiders (Vink & Paterson 2003, Ivanov *et al.* 2018, 2021) and (7) the broader objectives of the study the wolf spider radiation at the scale of the Pacific, including the already know phylogeny of the Galapagos wolf spiders.

Wolf spider phylogenetic studies have recently shifted from single locus (e.g., Zehethofer & Sturmbauer, 1998; Vink *et al.*, 2002) to multilocus studies using the genes 12S, NADH, 28S and COI (Murphy *et al.* 2006, Planas *et al.* 2013, De Busschere *et al.* 2015, Piacentini & Ramírez 2019). The use of genomic-scale approaches has just started in systematic studies (Ivanov *et al.* 2018, 2021).

12S and NADH1 are genes known to be useful to resolve relationships between closely related genera but are too conservative for adequate resolution at species level (Zehethofer & Sturmbauer 1998, Hedin & Maddison 2001, Vink *et al.* 2002, Vink & Mitchell 2002). 28S is also

known to resolve deep relationships, e.g., at the family level (Vink *et al.* 2002) but recent molecular attempts found that Lycosidae contains paralogous copies of the 28S, making it unsuitable for phylogenetic analysis (Murphy *et al.* 2006). By contrast, COI is a widely used gene that usually performs well in taxonomic assignments, be it between closely related species, genera, or subfamilies. However, COI trees have been observed to conflicted conspicuously with trees computed from other genes or parts of the mitochondrion (NADH1, 16S, 28S) (Vink & Paterson 2003). Moreover, and while nuclear protein-coding genes like Actin 5C and Histone 3 have not been extensively used in wolf spider phylogenetic analyses, they have proven to be useful in resolving the radiation of the Galapagos wolf spiders (De Busschere *et al.* 2012, 2015).

Recently, Krehenwinkel *et al.* (2018) developed a set of primers and a simple multiplex PCR protocol for arthropod systematic and phylogeny by Illumina amplicon sequencing. Their primers were established as effective phylogenetic markers for spiders in general (Kennedy 2018, Krehenwinkel *et al.* 2018) and were used in this study (Table 4).

DNA extractions

The amount of material collected from specimens varies from one leg to the entire spider (juveniles), according to the size of the specimen. For small adult specimens, genitalia were removed and kept as a voucher. Specimens were dried on absorbent paper, the selected parts were cut off using sterile razor blades and put into a new 1.5 mL tube. Samples were weighed and then placed at -20°C until extraction. DNA was extracted using DNEasy Blood and Tissue kit (Qiagen) or Puregene Gentra kit (Qiagen). Extractions using DNEasy Blood and Tissue kit were done following the manufacturer's protocol slightly modified. Notably, samples were incubated for three hours at 56°C, the volume of ATL Buffer, proteinase K, Buffer AL, and Ethanol 100% were increased accordingly to the size of the specimen, two elutions in 50µL were realized in separate tubes, columns were incubated at 65°C for 3 min before the final centrifugation step, which was modified to 2 min at 9,000 rpm. When using Puregene Gentra kit, samples were frozen in liquid nitrogen and grind using micropestle before following the manufacturer's protocol slightly modified. Notably, samples were incubated at 55°C overnight (at least 15 hours) with Proteinase K, and 0.5µL of Glycogen was added to increase DNA precipitation. All museum samples were extracted using Puregene Gentra kit (Qiagen), in the same laboratory facilities as recent specimens but their extractions took place months later to ensure that there were no recent DNA remnants. Moreover, extraction sessions were spaced in time to reduce cross-contamination pressure. The small amount of material and the poor state of conservation of most of the museum specimens did not allow the extraction to be replicated. DNA concentrations and quality were assessed using a Nanodrop spectrophotometer and agarose gels, respectively.

Table 4: Targeted loci, primer combinations, primer sequences including Illumina sequencing tails, expected length and average amplicon length. The “*” close to the ID indicates the loci for which we interpreted the phylogenetic trees.

Region	Locus	ID	Primers	Sequence 5'-3'	Length (bp)	Average amplicon length	
Mitochondrial	COI	COI	mIColintF	ACACTCTTCCCTACACGACGCTCTCCGATCTGGWACWGGWTGAACWGTWTAYCCYCC	365	318	
			Fol-degen-rev	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTTANACYCNGGRTGNCCRAARAAYCA			
	CytB	CytB	CB3C	ACACTCTTCCCTACACGACGCTCTCCGATCTGAGGDGCHACHGTWATNACNAA	401	-	
			CB4A	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTRAARTATCATTCDGGTTGNATNTG			
	12SrDNA	12S	*	12SF1	ACACTCTTCCCTACACGACGCTCTCCGATCTNCHACTWTGTTACGACTT	424	400
			12SR1	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTAMTAGGATTAGATACCCT			
	16SrDNA	16S	*	16SF2	ACACTCTTCCCTACACGACGCTCTCCGATCTAATYCAACATCGAGGTCGCAA	371	315
			16SR2	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTTRACYGTRCWAAGGTAGCAT			
	18SrDNA	18S_A	*	SSU_FO4	ACACTCTTCCCTACACGACGCTCTCCGATCTGCTTGCTCTCAAAGATTAAGCC	421	371
			SSU_R22	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTGCCTGCTGCCTTCCTTGGA			
18SrDNA	18S_B	*	18s_2F	ACACTCTTCCCTACACGACGCTCTCCGATCTAACTTAAAGRAATTGACGGA	351	272	
		18s_4R	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTCKRAGGGCATYACWGACCTGTTAT				
28SrDNA	28S	*	28s_3F	ACACTCTTCCCTACACGACGCTCTCCGATCTTTTTGGTAAGCAGAACTGGYG	363	314	
		28s_4R	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTABTYGCTACTRCCACYRAGATC				
ITS2	ITS2	*	5.8S3F	ACACTCTTCCCTACACGACGCTCTCCGATCTATCACTHGGCTCRYGGRTCGATG	436	435	
		28S2R	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTTCTTTCTCCSCTHANTDATATGC				
Histone H3	H3		H3aF	ACACTCTTCCCTACACGACGCTCTCCGATCTATGGCTCGTACCAAGCAGACVGC	374	328	
			H3aR	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTATATCCTTRGGCATRATRGTGAC			
Actin 5	Act5		Actin2_F2	ACACTCTTCCCTACACGACGCTCTCCGATCTGAYTTYGARCARGARATGGCNAC	270	226	
			Actin2_R1	GTGACTGGAGTTCAGACGTGTGCTCTCCGATCTGRTCDGCAATNCCWGGRTACAT			

PCR amplifications

PCR was used to amplify a total of nine markers (summarized in Table 4), of which one was protein-coding mitochondrial markers (Cytochrome B (Cyt B) and Cytochrome Oxidase I (COI)), two protein-coding nuclear markers (Actin 5 (Act5) and Histone H3 (H3)), two non-coding ribosomal mitochondrial markers (12S and 16S), and three non-coding ribosomal nuclear markers (18S, 28S and ITS2). PCR primers contained 5'-tails from Illumina to perform a subsequent indexing PCR.

DNA samples were standardized to 10 ng/μL except those whose initial concentration was lower than 100 ng/μL (estimated by Nanodrop), which were not diluted. Recovery of the primers was tested primer per primer and in two multiplex PCR, one grouping the mitochondrial primers (COI 12S and 16S) and another the nuclear primers (Act5, H3, 18S, 28S, ITS2). PCR tests were conducted on a subset of samples using the Multiplex PCR kit (Qiagen) following the manufacturer's protocol and Krehenwinkel *et al.* (2018) annealing temperatures: initial denaturation of 15 min at 95°C; 25 cycles of: a denaturation step of 30 sec at 94°C, an annealing step of 1min 30 sec at 46°C for mitochondrial genes and 55°C for nuclear genes, an extension step of 1 min 30 sec at 72°C; and a final extension of 10 min at 72°C. PCRs were run in 15μL containing 1X of Qiagen Multiplex Master Mix, 0.2μM of each primer and 1.5μL of DNA (0.2 to 10 ng/μL final). Amplification control was done using agaroses gel. Amplifications were low and we tested the recovery of these genes using gradient PCRs (annealing temperatures from 46 to 55°C for mitochondrial and from 52 to 61°C for nuclear), a different number of cycles (25, 35 and 40 cycles) and with and without the Q solution (Qiagen). The optimal conditions were obtained at the same annealing temperatures as those found by Krehenwinkel *et al.* (2018), 46°C for mitochondrial and 55°C for nuclear, but using 40 cycles. Increasing the number of PCR cycles above routine 20-30 cycles is a common practice when working with old-type specimens but can raise the number of polymerase errors. However, a recent publication demonstrated that there is no relationship between the number of PCR cycles (up to 55 cycles were tested) and the number of mutations in the context of high throughput DNA barcoding using Illumina MiSeq sequencing (Vierna *et al.* 2017). Even optimal PCR conditions produced some non-specific amplifications. There were additional amplicons for all the markers except Act5 (see Table S2). These multiple amplifications are related to the design of the primers which are very generalist. However, as we used MiSeq sequencing, these additional amplicons were not considered problematic as we would be able to sort them out of our sequences just by looking at their length + as we are using a 2 x 300 bp chemistry for MiSeq sequencing, longer sequences won't be sequenced.

Finally, all specimens were amplified for the two multiplexes. A selected subset of museum specimens was duplicated during PCR: samples were amplified from different PCR mix, on different days. Controlled were included (PCR mix + water) in each day of amplifications. PCR

products were quantified on an agarose gel relative to a DNA ladder (Promega) and based on band intensity. Based on the relative quantification, we pooled approximately equal amounts of PCR product from the same specimen for the two multiplexes PCR into a single well.

Library preparation, clean-up and sequencing

Samples were transferred to the Human and Environmental Genomic platform of the University of Rennes 1 (Rennes, FRANCE) for library preparation, cleaning and sequencing using MiSeq. PCR products were cleaned of residual primer using 1X AMPure Beads XP (Beckman Coulter). The purified PCR products have been quantified using Quanti-IT Picogreen dsDNA Assay kit (Invitrogen) and qualified using an BioAnalyzer (Agilent). Indexing PCRs of 6-11 cycles were performed using a SmartChip (WaferGen) on pooled amplicons, with indexing primers binding to 5'-tails of the locus-specific PCR primers to introduce dual indexes and Illumina sequencing adapters. For each PCR sample, a unique combination of forward and reverse primers was used so that the sample could later be identified from the sequencing run. The indexed products were cleaned up and quantified by qPCR, then all pooled in equal amounts into a single tube and sequenced on an Illumina MiSeq using V3 (600 cycles) chemistry and 2 x 300 bp reads.

Sequence processing

Sequences were demultiplexed by index barcode combination. We merged paired reads using PEAR (Paired-End reAd mergeR; Zhang *et al.* 2014) with a minimum overlap of 50bp and a minimum quality of Q20. Merged reads were then quality filtered ($\geq 90\%$ of bases $\geq Q30$) and converted into fasta files using the FastX Toolkit (Gordon & Hannon 2010). The resulting fasta files were demultiplexed by primer pair (i.e., target locus), by filtering sequences that start with the forward and end with the reverse primer sequence for each locus. Sequences were clustered into operational taxonomic units (OTUs) using USEARCH (Edgar 2010) at 97% similarity threshold (*cluster_otus*) for COI, Act5, H3, 12S and 16S loci; and treating every truly unique sequence as a separate OTU (*unoise3*), called a zero-radius OTU, for the ribosomal nuclear loci (18S, 28S and ITS2), as they contained heterozygote sequences. A de novo Chimera removal step was included in the clustering. We excluded all OTUs with less than 4-fold coverage. We also excluded all OTUs with less than 10 reads, as 10 reads proved to be sufficient to reliably call consensus sequences from amplicon sequencing data (Henrik Krehenwinkel, comm. pers.). Because of sequencing error, heterozygosity, co-amplification of taxa associated with the targeted spiders, e.g., parasites such as fungi or nematodes, and NUMTs (mitochondrial sequences transposed into the nuclear genome), most of the specimens had more than one OTU for a given marker. The resulting OTU were thus compared against the NCBI nucleotide database using BLASTn (Altschul *et al.* 1990) to filter out non-spider sequences. NUMTs were identified in protein-coding markers (COI, Act5 and H3) by translating the sequences and finding OTU sequences that were interrupted by a stop codon. Some specimens showed spurious amplicons (possibly NUMTs), which were considerably

shorter than the expected length of the sequence. There were also excluded. After these initial filtering steps, it was generally easy to identify the correct OTU as the one with the largest number of reads. After these initial filtering steps, it was easy to identify the correct OTU as the one with the largest number of reads for COI, Act5 and H3. However, for most specimens for the other markers, OTU size was not sufficient to distinguish correct from incorrect OTUs and a neighbor-joining tree was built using all specimens. From these trees, erroneous and heterozygous sequences could be more easily recognized because they fell outside of clades formed by conspecific specimens. Once a single correct sequence had been identified for each marker from each specimen, sequences were aligned in Geneious Prime 2012.2.1 (<https://www.geneious.com>) using the Geneious alignment tool. Alignments were then further checked by hand. Because of incongruencies between mitochondrial genes (although no recombination of the mitochondrial genome of Lycosidae is known), we re-aligned the mitochondrial genes in MEGA7 (Kumar *et al.* 2016) using ClustalW (Thompson *et al.* 1994) with the default values (15 for gap opening and 6.66 for gap extension; 0.5 for transition weight), which were further checked by hand.

Phylogenetic analysis

We analyzed all markers separately to check for incongruencies between loci using Maximum Likelihood (ML) on the CIPRES Science Gateway (<https://www.phylo.org/portal2/home.action>, (Miller *et al.* 2010)). ML phylogenetic reconstructions were first generated using RAxML-HPC v.8 (Stamatakis 2014) but gave low support values (results not shown). We then generated using IQ-Tree 2.1.2 (Nguyen *et al.* 2015) with ultrafast bootstrapping (Minh *et al.* 2013) which allowed us to get slightly more supported nodes of the phylogenetic trees. We used ModelFinder (Kalyaanamoorthy *et al.* 2017) to identify substitution models for each locus (with lowest AICc value, Table 5). Trees were rooted with Hawaiian Lycosidae of another family (supposedly Artoriinae) and the Pisauridae *Bradystichus crispatus*. Trees were edited using TreeGraph 2 (Stöver & Müller 2010).

Results

The wolf spiders collected for this study constitute the most complete collection from the Hawaiian archipelago so far. However, they do not evenly cover the islands of the archipelago nor the elevations. Hence, the phylogenies it depicted are partial views of the actual wolf spider diversity.

Among the 239 Hawaiian wolf spiders that we sequenced, 33 did not work, probably because DNA degradation prevented sequencing, and some contamination. Due to questionable placement, the sequences obtained from a priori Artoriinae, the Museum specimens of *Syroloma* and *Lycosella*, are not included in these preliminary results. However, sequences from fresh non-identified wolf spiders were located out of the tree (and grouped with actual Artoriinae in phylogenetic trees including published sequences, results not shown).

The statistics for each locus are given in Table 5. The different loci were not obtained uniformly for all samples with sequencing success ranging from 21% (Histone 3) to 83% (16S). Considering the very few samples successfully sequenced with Histone 3 and Actin 5, we had to exclude these loci from our analysis. The mitochondrial loci (COI, 12S, and 16S) and the nuclear locus ITS2 present the lowest pairwise identities between sequences (90% to 93%) and will thus probably carry more phylogenetic information than the other loci which are less variable with sequences similar from 96 to 98%.

Table 5: Summary of the characteristics of the nine loci targeted in this study. Sequencing success means the percentage of samples for which sequences we were in good condition enough to be used in the phylogenetic reconstruction compared to the total number of samples for which we got sequences (206). Pairwise identity was calculated by the Geneious software on the alignment of each locus.

	Mitochondrial			ITS2	28S	Nuclear		H3	Act5
	COI	12S	16S			18S_A	18S_B		
Sequencing success (total 206)	76%	73%	83%	68%	63%	71%	79%	21%	28%
Nb of sequences per locus	156	151	172	140	130	146	163	44	57
Pairwise identity of sequences	90.1%	91.4%	93%	92.1%	97.9%	98.1%	98.1%	96%	96.4%
Selected model of substitution (AIC, ModelFinder)	TIM3 + F + I + G4	TIM + F + I + G4	TIM3 + F + G4	TIM2 + F + G4	TN + F + G	TNe + G4	K2P + R2	-	-

Inter- and among islands phylogenetic relationships

When doing the phylogenetic reconstruction for the nuclear loci (ITS2, 28S, 18S_A, and 18S_B), we realized that two different paralogous copies were retained during the OTU selection, for each locus. This was shown by two divergent groups on the trees. Unfortunately, I did not

have time to go back to the OTU selection for these preliminary results. Only a few samples were concerned for the ITS2 and 28S. Thus, I will try to carefully draw up the main patterns given by these phylogenies, considering the two potential copies or excluding the one we consider paralogous. On the opposite, for 18S_A and 18S_B, the samples divide into two copies so we prefer not to interpret their results (but the tree are shown in supplementary material, Figures S2 and S3).

The broad tree topologies obtained by the 7 loci show some incongruities, between mitochondrial and nuclear trees, and in a smaller dimension between mitochondrial trees (see Figures 4 and 5). Consequently, the topology of the COI tree is detailed and the topologies of the trees obtained from the other loci are compared to it as COI is supposed to give the best resolution between closely related species.

Because the surface wolf spiders sequenced were collected from a large range of elevations (see Table 2), three categories of altitudes were arbitrarily defined: low altitude (0-1000m), medium-altitude (1000-2000m), and high altitude (above 2000m), to help the understanding of the phylogenetic patterns.

Mitochondrial loci

COI

The COI tree (Figure 4B), is weakly resolved, which is shown by its short branches. Nonetheless, it shows a hierarchical organization of the spiders from the Hawaiian archipelago. Spiders group according to their habitat (cave vs. surface), island and altitudes with:

- **1.** A group of **cave wolf spiders from the island of Hawaii** (bootstrap: 100) including 3 different cave systems and a surface wolf spider found at low elevation (938 m) in a tropical wet forest of the Mauna Loa volcano (HaML2). This group clusters with the European species *Hogna radiata*.

- And a group of **surface wolf spiders**. This one includes three main groups:
 - **2.** A group of **wolf spiders was found at low altitudes (0-900m)** (bootstrap: 99) **on the islands of Kauai, Oahu, and Molokai**. In this group is found a spider identified as *Hogna crispipes* (OaWa11).

 - **3.** A group of **wolf spiders was found on the island of Maui** (bootstrap: 74).

- A group of **wolf spiders was mainly found on the island of Hawaii** (bootstrap: 85). This group divides into at least 2 sub-groups:
 - One sub-group of spiders coming from the medium to high elevations of the **Mauna Kea and Mauna Loa volcanoes** (bootstrap: 97) splits into two clusters:
 - ❖ 4. One mainly from **high altitudes to summit (2800-4000m) on the Mauna Kea volcano** (bootstrap: 86) which also **includes two spiders from medium altitudes (1220 m)** collected on the Mauna Loa volcano.
 - ❖ 5. One from **medium to high altitudes (1600-3048m) on the Mauna Loa volcano** (bootstrap: 97).
 - One sub-groups of spiders coming from low to high altitudes from the **Mauna Kea, Mauna Loa and Kilauea volcanoes** with low support value (bootstrap: 66) including:
 - ❖ 6. One from **medium to high altitudes (1500-2400m) on the Mauna Kea, Mauna Loa and Kilauea volcanoes** (bootstrap: 95).
 - ❖ 7. One from **low to medium altitudes (900-2400m) of the Kilauea volcano** (bootstrap: 97).
 - ❖ 8. A bush from **medium to high altitude (1524-3000m) of the Mauna Kea and Mauna Loa volcanoes, and from Oahu (OaWa10)**.
 - ❖ 9. A second bush, more basal, of **low to high altitude (950-2400m) from Mauna Loa and Kilauea spiders, including a group (9b) of spiders from low altitude on Kilauea (300m) and medium-altitude on Mauna Loa (1750-2000m)** (bootstrap: 82).

In summary, based on the COI, we distinguish a well-separated lineage of cave spiders and a second lineage of surface spiders. In this surface lineage, we found three groups: one of the spiders from low altitude on the islands of Kauai, Oahu and Molokai; one from the island of Maui; and one of spiders coming mainly from Hawaii.

Comparison of 16S and 12S to the COI tree

The 16S and 12S trees also separate cave from surface wolf spiders (Figure 4, A and C). The placement of the groups and their relationships however are not all the same.

The cave spider group was not well recovered by the tree of the 12S (Figure 4, C), but most of the cave spiders were not successfully sequenced for this locus. 12S does not recover a single cave spiders group but two separate groups, one grouping with the outgroups (HaML1 and HaMK1) (Figure 4C). Interestingly, a surface specimen (HaMK1) from the surface of the Mauna Kea volcano, for which we did not get any sequence with the other mitochondrial loci, groups with a cave spider (HaML1). From the 16S tree, however, we got the same group as with COI, and more resolution was brought by the successful sequencing of a representative of the blind species from the island of Kauai: *Adelocosa anops* (Kauai7).

For surface spiders, 16S does not recover a lineage of mainly Hawaiian spiders as COI and 12S as the Maui group belongs to the same lineage in the 16S tree. Moreover, the two groups that were distinguishable among the Hawaiian surface spiders with COI, one composed of the groups 4 and 5 (high altitude Mauna Kea and Mauna Loa volcanoes) and the other one the groups 6 to 9 (low to high altitude, three volcanoes), differ within the 16S and 12S. With these slowly evolving loci, the two groups are: one composed of group 4, 9 and 5, and the other one of groups 6 to 8. One museum specimen, HaML22 identified as *Hogna oahuensis* (Gertsch determination), was recovered with 12S and 16S and group into group 4. Another museum specimen, Maui 13 identified as *Lycosella* sp., was recovered with 12S and group into the second group of Maui spiders (3b).

Comparison of nuclear 28S and ITS2 to the COI tree

The trees obtained by the nuclear loci 28S and ITS2 are less resolved than the ones obtained by the mitochondrial loci (Figure 5).

The 28S tree (Figure 5A) did not recover all our outgroups with some of the samples which were previously really basal in the mitochondrial trees (e.g. HaMK32) which group within the surface Lycosinae. On the opposite, the cave spiders, be them recovered as a group (bootstrap: 88), is basal to the tree. The surface wolf spider HaML2 which was previously grouping with the cave spiders does not group with them when looking at the 28S tree but is located in between the cave and the surface spiders.

For the ITS2 tree (Figure 5B), some of the outgroups are also located within the surface Lycosinae (e.g. HaMK 32, HaMK33) but the other outgroup specimens are still basal to the tree. The cave spiders are recovered as a separate lineage within the Lycosinae, except for one of the samples (HaML1) which group with the outgroups and with a spider from the surface of the Mauna Kea volcano in particular (HaMK1).

Concerning the surface spiders, most of the groups previously identified with COI, 16S and 12S are not found with the nuclear loci at the exception of the Maui group (bootstrap: 93 for 28S, 70 for ITS2). The group of spiders found at low altitudes on the islands of Kauai, Oahu and Molokai

is not properly recovered as it is split into multiple groups and some of the spiders previously belonging to this group fell into the unresolved bushes of the trees obtained by the nuclear loci. One museum specimen, OaWa7 identified as *Hogna hawaiiensis* (Roth determination), as well as another one identified as *Hogna crispipes* (OaWa2) are recovered into the group of low altitude wolf spiders on the islands of Kauai, Oahu and Molokai with ITS2.

Phylogenetic relationships of the cave wolf spiders

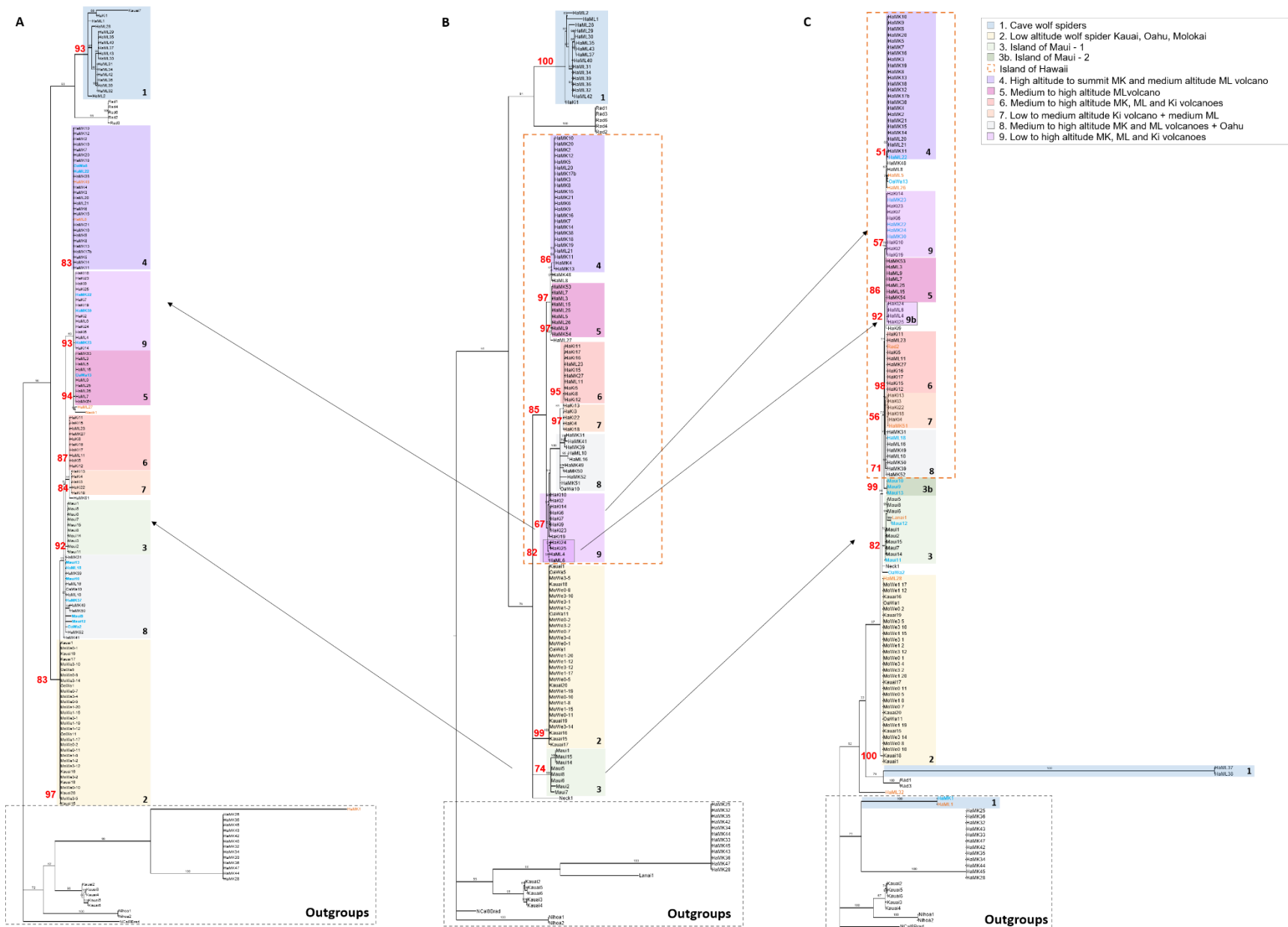
The cave wolf spider group has been recovered with six of the seven loci studied. We here focus on the relationships of the samples using the subtrees obtained from the COI and the 16S loci (Figure 6A and B).

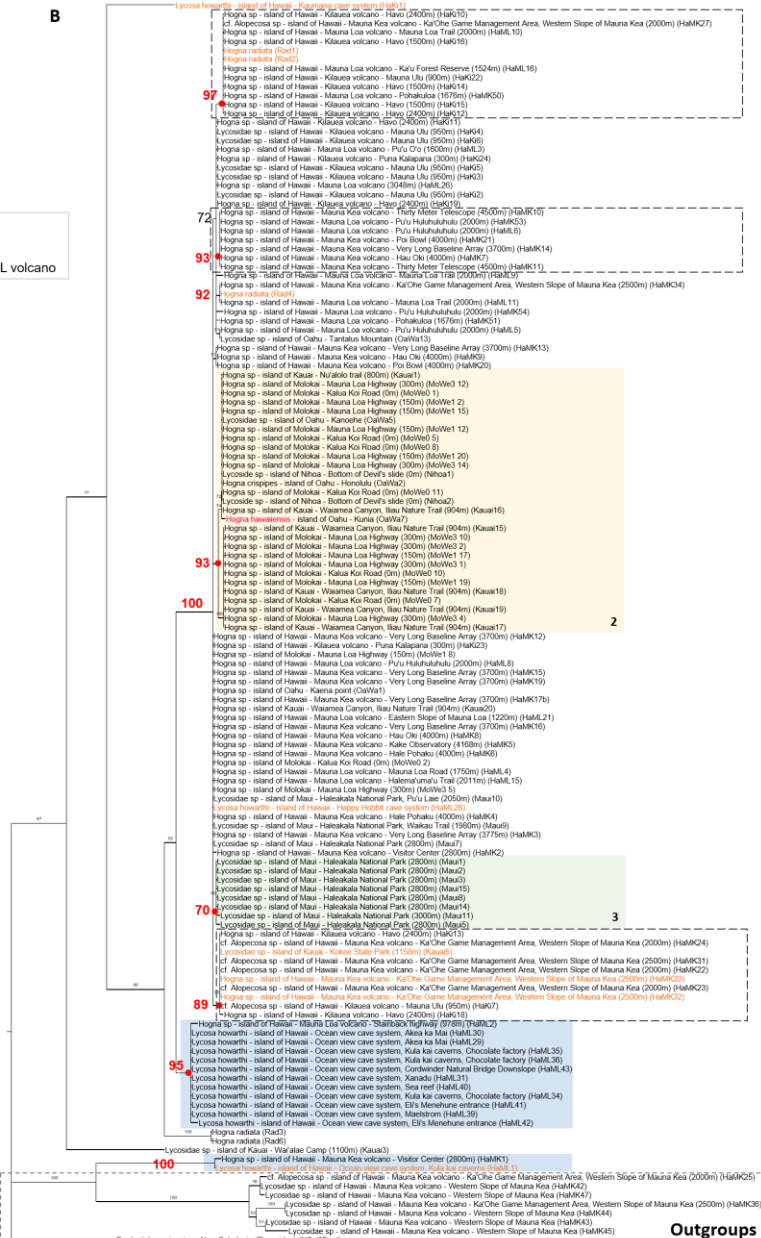
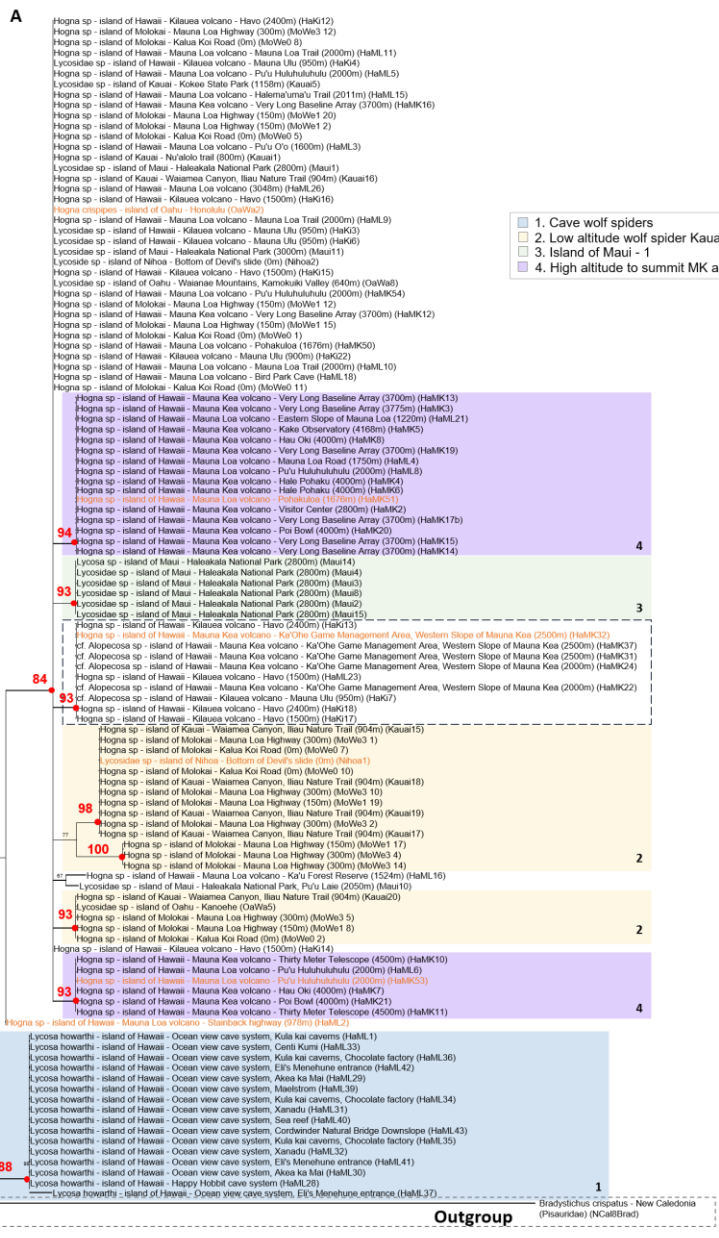
The relationships within the cave lineage follow the cave systems with the spider from the Kaumana cave system (youngest cave studied) being separated from the one from the Keokeo and Kipuka Kanohina Cave systems. The spider from the Keokeo cave system seems to be older than the ones from the Kipuka Kanohina cave system, which is consistent with the age of the caves (see Table 3). We had several samples from the Kipuka Kanohina cave system which, in turn, separate into two groups, with specimens coming from the same cave splitted into these two groups (e.g. HaML34 and HaML35), plus a specimen which is isolated (HaML1).

When a sequence of *Adelocosa anops*, the blind cave spider from Kauai, was successfully sequenced (16S, Figure 6B), it fell into the cave group and seems to be related to the spider (HaKi1) from the Kaumana cave (youngest cave studied).

Interestingly, with COI, 16S, and ITS2, the surface spider HaML2, collected on a wet forest at low elevation of Mauna Loa volcano fell into the cave group. With 12S and ITS2, a second surface spider, HaMK1, was collected on the lava flows of the Mauna Kea volcano, group with one spider from the cave system Kipuka Kanohina (HaML1), from the Kula Kai caverns.

Figure 4: Maximum likelihood phylogeny of Hawaiian wolf spiders from the (A) 16S, (B) COI, and (C) 16 loci. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support value of the groups of interest are highlighted in red. In the 16S and 12S are written in blue the samples which were not successfully sequenced by COI and in orange the samples with different placement. For reasons of space we did not show the information about the samples (identification if ever, location, elevation) but only their code. Their information can be found in Table S1. →





← **Figure 5:** Maximum likelihood phylogeny of Hawaiian wolf spiders from the A) 28S and, B) ITS2 loci. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support values of the groups of interest are highlighted in red. Are written in orange the samples with different placement compared to COI. The boxes in black dotted lines represent groups that were not recovered by COI nor 16S or 12S.

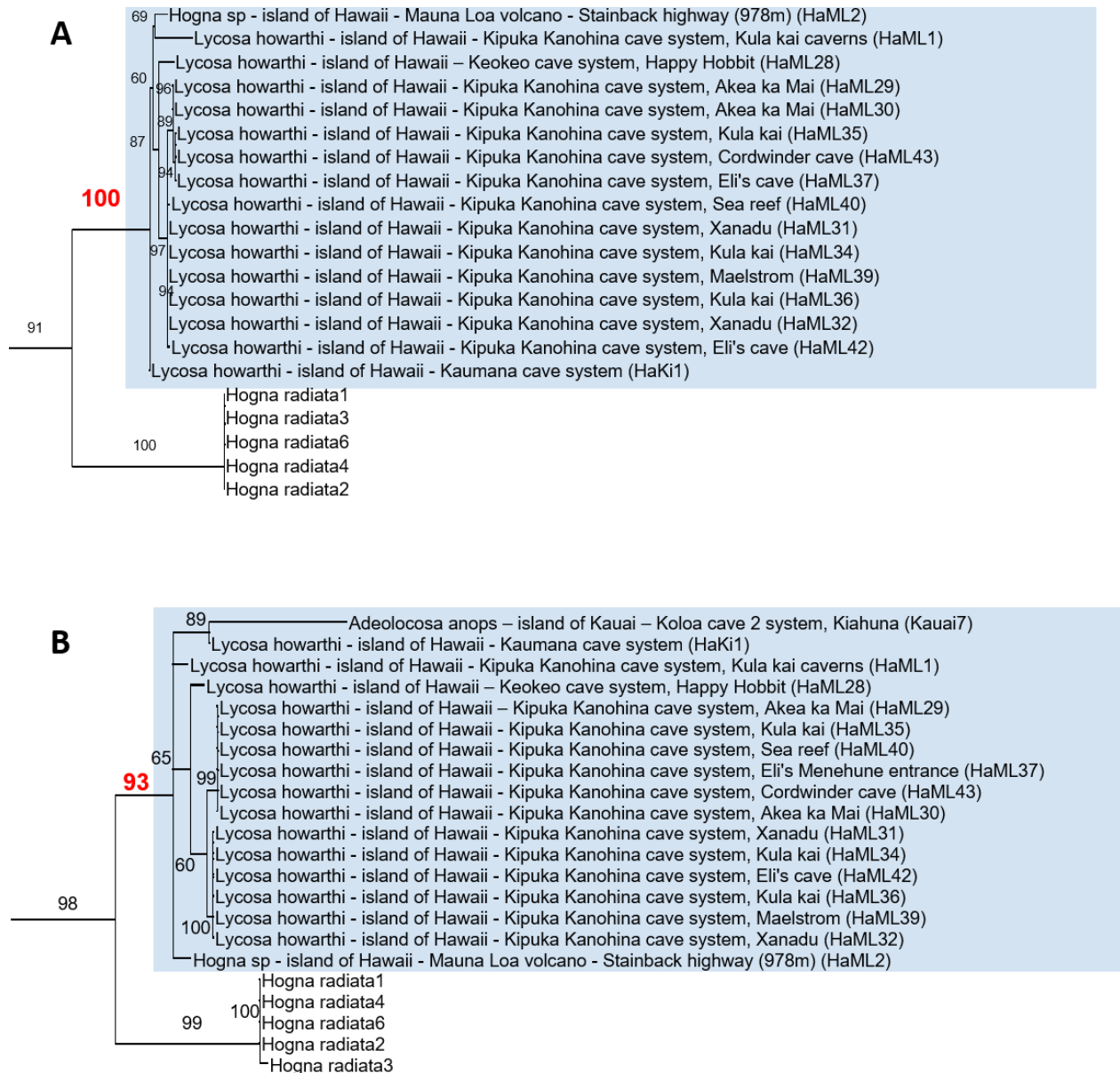


Figure 6: Maximum likelihood phylogeny of the cave wolf spiders from (A) COI and (B) 16S loci. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support values of the group of interest are highlighted in red.

Discussion

Our preliminary phylogenetic analysis of the wolf spiders from the main islands of the Hawaiian archipelago based on COI, 16S, 12S, 28S and ITS2 shows relatively low support and some incongruities between loci (which are discussed in the part Conflicting phylogenies below). Limits between populations and species need to be investigated in the near future (see the perspectives section below).

Phylogenetic relationships

Our phylogenies show relatively low resolution, low support and incongruities between loci. This suggests that (1) the radiation of the Hawaiian wolf spider is recent and the loci we used do not evolve fast enough to carry informative variation and resolve the relationships within this group, and/or (2) there is hybridization between lineages causing gene flow which removes the signal of divergence (Chung & Hey 2017). Because these wolf-spiders are among the first animals to colonize new lava flows (Howarth 1979, Crawford et al. 1995, Edwards & Thornton 2001), we suggest that they may disperse and be able to migrate to new substrates as these become available. Accordingly, the populations found at different elevations along the slope could exchange individuals, arguing in favor of gene flow avoiding divergence. Despite this, the results obtained in this study distinguish some lineages between islands, and between surface and cave spiders.

Overall, the Lycosinae wolf spiders from the Hawaiian Archipelago group all together and are well delimited from the outgroup we used. It splits in two: the surface wolf spiders on one side, the cave wolf spiders on the other. The cave wolf spider lineage has been recovered with six of the seven loci studied. It clusters close to the European species *Hogna radiata*, confirming its belonging to the subfamily Lycosinae (see the perspectives section for further investigation of the taxonomic placement of the Hawaiian wolf spiders). The Hawaiian cave wolf spider *Lycosa howarthi* clusters with the species *Adelocosa anops*, when its sequence was recovered, with little genetic variation, which questions their separation in two different genera.

Between islands

Our phylogenetic analysis recovers lineages with different distributions over the archipelago. One is restricted to the island of Maui. Two species of Lycosinae: *Hogna hawaiiensis* and *Alopecosa oahuensis*, are known from this island. Representatives of these species were included in the phylogenies but did not group within that lineage. We thus hypothesize that the lineage identified restricted to the island of Maui could be a new species, but this needs to be further tested (see the perspectives section). Another lineage recovered by our analysis is spread on the older islands: Kauai, Oahu and Molokai. This lineage presents very few genetic variations even if

it is spread on different islands. Moreover, one of the spiders was identified as *Hogna crispipes*, an introduced species distributed all over the Pacific (although representatives of *H. crispipes* from outside of the Hawaiian archipelago were sequenced but are not recovered within this lineage, results not shown). The specimens sequenced were all from low altitude (but some museum specimens did not have elevation recorded), where there is the most human activity. Consequently, we suggest that this lineage could be recent colonization of the archipelago. A third lineage identified with this phylogenetic analysis is dominated by spiders from the island of Hawaii (which are over-represented in our dataset), but also includes some spiders from Maui and Oahu.

These different aforementioned lineages are from islands of different ages, with the islands of Kauai (5.1 my), Oahu (3.7 my) and Molokai (1.8 my) being older than Maui (1.3 my) and Hawaii (0.5 my). There is however no evidence of progressive colonization of the spiders from the older islands to the youngest islands. Moreover, a lineage contains spiders from old and young islands. Nevertheless, the collection of samples we sequenced, despite containing spiders from almost all the main islands, was not exhaustive (especially because the wolf spiders from the island of Hawaii were over-represented). Nonetheless, in the current state of our understanding, these relationships between the lineages studied here suggest that there might have been several independent colonization of the Hawaiian archipelago by spiders who settled on different islands. The distribution of one lineage between three islands (Kauai, Oahu and Molokai), and the presence of some spiders from Oahu in the lineage identified as mainly from Hawaii highlights a high dispersal capacity. This pattern, if confirmed, will be interesting as different from the progression pattern found for other Hawaiian spider radiations, e.g. *Orsonwelles* (Linyphiidae), *Ariamnes* (Theridiidae), *Mecaphesa* (Thomisidae) and *Tetragnatha* (Tetragnathidae) (Gillespie *et al.* 1997, 2018, Hormiga *et al.* 2003, Garb & Gillespie 2009). A progression rule (or pattern) refers to a phenomenon of phylogeographic concordance with island age, whereby older lineages map to older islands within an archipelago, and younger lineages map to progressively younger islands in that system (Wagner & Funk 1995, Shaw & Gillespie 2016).

Between altitudes

The large sampling of wolf spiders from the island of Hawaii across different volcanoes and a wide range of elevations allowed us to test the hypothesis of differentiation of the Hawaiian wolf spiders according to altitude. The Hawaiian lineage shows a complex phylogenetic pattern with very short branches and variation of groups placement according to the locus studied. Delineation of independent lineages based on the molecular data produced during this study appears difficult. From the mitochondrial loci, we distinguished a group of rather high altitude spiders coming from the volcanoes of Mauna Kea and Mauna Loa and a second from low to high altitudes from the three volcanoes (Mauna Kea, Mauna Loa and Kilauea). Such grouping was not recovered with the nuclear loci, what can be explained by the smaller effective population size of mitochondrial

genes means that makes them coalesce more quickly; and second, by the fact that mitochondrial genes do not recombine. Consequently, there is no clear pattern according to volcano nor altitude, although at least three different bulbs (male genitalia) were observed during previous investigations (Julien Pétilion, comm. pers.). This suggests that the spiders from different elevations and volcanoes might not be fully reproductively isolated from each other and might be still exchanging individuals (and gene flow). Another wolf spider radiation of the genus *Hogna* is known in the Pacific, from the Galapagos archipelago. De Busschere *et al.* (2010, 2012, 2015) found speciation related to habitat specialization (wet habitats vs. upland pampa vs. lowland coastal arid habitats) within islands, repeated on each island of the archipelago, under historic gene flow. This pattern is not found here on the main islands of the Hawaiian archipelago, although they are older (5.1 to 0.6 my) than the Galapagos archipelago (3.2 to 0.7 my), so early colonists of the Hawaiian archipelago could have had more time to diversify. This absence of speciation related to surface habitat specialization on the Hawaiian archipelago could be related to the fact that the surface habitat colonized by wolf spiders are not contrasted enough (high Aeolian vs. neogeoaelian) to cause ecological speciation.

Among the cave spiders

The lineage (mainly composed of *Lycosa howarthi*) shows some genetic variation. The spiders cluster according to their cave system but they also seem to start differentiating within the cave system which was the more covered in our study (Kipuka Kanohina cave system) as some *Lycosa howarthi* collected on the same caves of this system are found to fall into two different groups. A study conducted on Hawaiian cave planthoppers (Wessel *et al.* 2013) showed that these cavernicol exhibit one of the highest speciation rates, suggesting that the conditions down to the Hawaiian caves are conducive to diversification. A study conducted on troglobite spiders of the genus *Dysdera* (Dysderidae) (Arnedo *et al.* 2007) showed that there might be sympatric speciation among troglobitic spiders inhabiting the same caves, potentially through trophic segregation. However, this is unlikely in *L. howarthi* which is known to freely exploit resources in larger cave passages (contrary to other inhabitants of the same caves, see Howarth 1983). On the other hand, cave-adapted species often have reduced dispersal powers (Howarth 1993) and there might also be barriers to subterranean dispersal such as geological structure (Howarth 1983). The Hawaiian caves studied here are part of one of the longest (Kazumura caves) and the third longest (Kipuka Kanohina) cave systems in the world (<http://www.caverbob.com/lava.htm>). Therefore, we suggest that limited dispersal might be a driver of segregation (not to say speciation, as limits between populations and species have not been tested here).

Our study failed to test the relationship between *Adelocosa anops* and potential surface relatives from the island of Kauai from the few representatives of Kauai we had in our dataset and from the absence of specimens of *Hogna likelikeae*. However, it showed that *Adelocosa anops*

seems to be related to one cave wolf spider from the youngest cave we studied, suggesting colonization of this young cave by a species closer to *Adelocosa anops* than the other *Lycosa howarthi*. Troglobites usually do not disperse on the surface, although such dispersal may occur under species circumstances or as rare chance event (see Howarth 1983 and references therein). It is therefore unlikely that specimens of *Adelocosa anops* colonized this cave.

On this cave lineage are found at least two specimens from the surface of the island of Hawaii. Their presence in this lineage suggests that adaptation to cave environment could be evolutionarily labile for these wolf spiders. It is surprising that on the 133 specimens we gathered from this island, only two seem to be related to the cave lineage. This relationship of surface and cave (*L. howarthi*) wolf spiders from the island of Hawaii, associated with the close relationship of *L. howarthi* with *A. anops* let us suggest that *A. anops* could also be related to surface spiders of its island (Kauai). It is necessary to continue to investigate the relationships between these two troglobitic wolf spiders and their surface relatives with additional sampling from the islands, other than Hawaii. It would also be interesting to including to these investigations specimens of the third known troglobitic wolf spiders, *Nukuhiva adamsoni*, from the Marquesas Islands, to determine how a third event of cave-adapted wolf spiders occurred in the Pacific.

Conflicting phylogenies

The incongruences found on the phylogenies reconstruct from the different loci we targeted illustrated the fact that monophyly depends on the gene region you look at, as impressively shown by the study of 20 genome assemblies in the rapidly radiation *Heliconius* butterflies (Edelman *et al.* 2019).

We observed incongruences among the phylogenies obtained by the different mitochondrial regions we studied. The mitochondrial genomes typically thought not to undergo recombination, so the entire mitogenome should have the same underlying gene tree (Masta 2000, Masta & Boore 2008, Meiklejohn *et al.* 2014). However, it is not rare that mitochondrial regions show incongruencies (Funk & Omland 2003). Part of these incongruities observed between the loci we targeted could be related to the fact that not all the samples were successfully sequenced for all the loci, changing consequently the topologies of the trees obtained from different loci. Another hypothesis explaining the incongruences could be a recombination of the mitochondrial genomes in these spiders. Although mitochondrial recombination may be highest as hybrid zones (Saville *et al.* 1998) and is known from other animals (e.g. birds, Meiklejohn *et al.* 2014), this hypothesis is certainly unlikely.

On the other hand, different genes (or portion of the mitochondrion), may show different speed of evolution (e.g. Mueller 2006). For example, COI is known to evolve faster than 12S and 16S, that could lead of them giving different phylogenetic patterns. Moreover, if the COI loci has been widely used to delimitate species (Hebert *et al.* 2003), it has proven to be problematic in

wolf spiders where it does not recover the species delimited on morphology (Astrin *et al.* 2016, Blagoev *et al.* 2016).

Discordance was also found between the mitochondrial and nuclear loci we targeted. Mitonuclear discordance is common in animals (Toews & Brelsford 2012). Several reasons might explain mitonuclear discordance: the smaller effective population size of mitochondrial genes means that makes them coalesce more quickly; the fact that mitochondrial genes do not recombine, while the nuclear genes do. Additional reasons have been summarized by Ivanov *et al.* (2018) such as horizontal gene transfer (HGT, e.g., Bergthorsson *et al.* 2003, Soucy *et al.* 2015), androgenesis (Hedtke & Hillis 2011), unresolved phylogenetic polytomy (e.g., Caraballo *et al.* 2012), mitochondrial pseudogenes in nuclear DNA (NUMTs) (Leite 2012, Song *et al.* 2014), incomplete lineage sorting (ILS) and introgression (Toews & Brelsford 2012, Mutanen *et al.* 2016), and infection with bacteria like *Wolbachia* (Jiang *et al.* 2018). A recent genomic-scale study focused on mitonuclear discordance in 6 European wolf spider species and showed they were explained by historical or ongoing introgressive hybridization (Ivanov *et al.* 2018), which could also be the case for the Hawaiian wolf spiders.

Perspectives

Analysis done in this study constitute a frame for further studies about phylogenetic relationships among rapidly evolving wolf spider species. These results lead us to propose several avenues for the continuation of this study as well as for future studies.

In the near future, we will be doing additional analysis on these data:

- **Comparing the ML phylogenetic reconstruction with Bayesian reconstructions** (using MrBayes 3.2.7a (Ronquist *et al.* 2012) with 10 million generations) and doing phylogenetic analyses on **concatenated alignments**
- **Reconstructing haplotype network and calculating p-distances** to help to visualize the relationships between individuals, populations, and species intuitively, revealing insights about migration, population structure, and speciation (Garcia *et al.* 2021).
- **Species delimitation using several gene trees** using multispecies coalescent model (MSC) which allows to consider conflicting gene-tree and consequently reliable estimation of the species phylogeny even if the information at every locus is weak (Yang 2015).
- **Dating the speciation**, but it's not always possible to date the splits if there is gene flow.
- Running **Isolation with migration model** to distinguish between population splitting (drift) and gene flow and determine how fast populations diverge (Hey 2010).
- **Including the sequences from the Pacific** (this Ph.D. and Genbank) to test the hypothesis of multiple colonization of the Hawaiian archipelago by wolf spiders as well as the origins of their ancestors.

- **Including the sequences from by Piacentini Ramirez (2019)** who reconstruct the most complete phylogenetic tree of wolf spiders so far, including representatives of each subfamily. This will allow to determine the taxonomic placement of our wolf spiders.

We suggest the coming studies focusing on Hawaiian wolf spiders, or other potentially recent radiation of a young lineage to use genome-wide Next-Generation-Sequencing (NGS) to get a better resolution of the phylogenetic relationships. Among the myriad of NGS available, we consider that:

- (1) genome sequencing seems hardly reachable because of the cost and the difficulty to sequence so many samples, which will be necessary in similar cases where morphological conservatism does not allow previous taxonomic knowledge about the studied group.
- (2) enrichment, e.g. using Ultra conserved Elements (UCE), which has greatly helped the resolution of the spider tree of life recently (e.g. Kulkarni *et al.* 2020).
- (3) transcriptomes sequencing (Garrison *et al.* 2016, Fernández *et al.* 2018, Kallal *et al.* 2021) to resolve deep phylogenomic relationships between the Pacific wolf spiders.
- (4) RAD tags: which is a popular method for population genetic and phylogeographic studies and is preferred over microsatellites approaches because of the limitations of their development due to the difficulty to find reliable loci (Brewer *et al.* 2014). Additionally, this method has recently proven to be relevant to delimit species and populations of closely related wolf spiders (De Corte 2016, Ivanov *et al.* 2021).
- (5) Genome skimming: which allows the assembly of plastid or mitochondrial genomes which is cheaper than any of the approaches mentioned before and would allow to sequence degraded DNA, such as from museum specimens (Coissac, Hollingsworth, Lavergne, & Taberlet 2016, Dodsworth 2015).

Conclusion

Finally, this study was the first to investigate the relationships among the Hawaiian surface and caves wolf spiders coming from different islands. The preliminary results presented here showed recent radiation driven by dispersal and habitat speciation likely mixed by gene flow. We found an independent lineage of cave spiders including some surface spiders suggesting that adaptation to cave is quite evolutionarily labile for these spiders. No clear pattern of elevational speciation was found but further analyzes are needed to better understand the situation.

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Supplementary materials

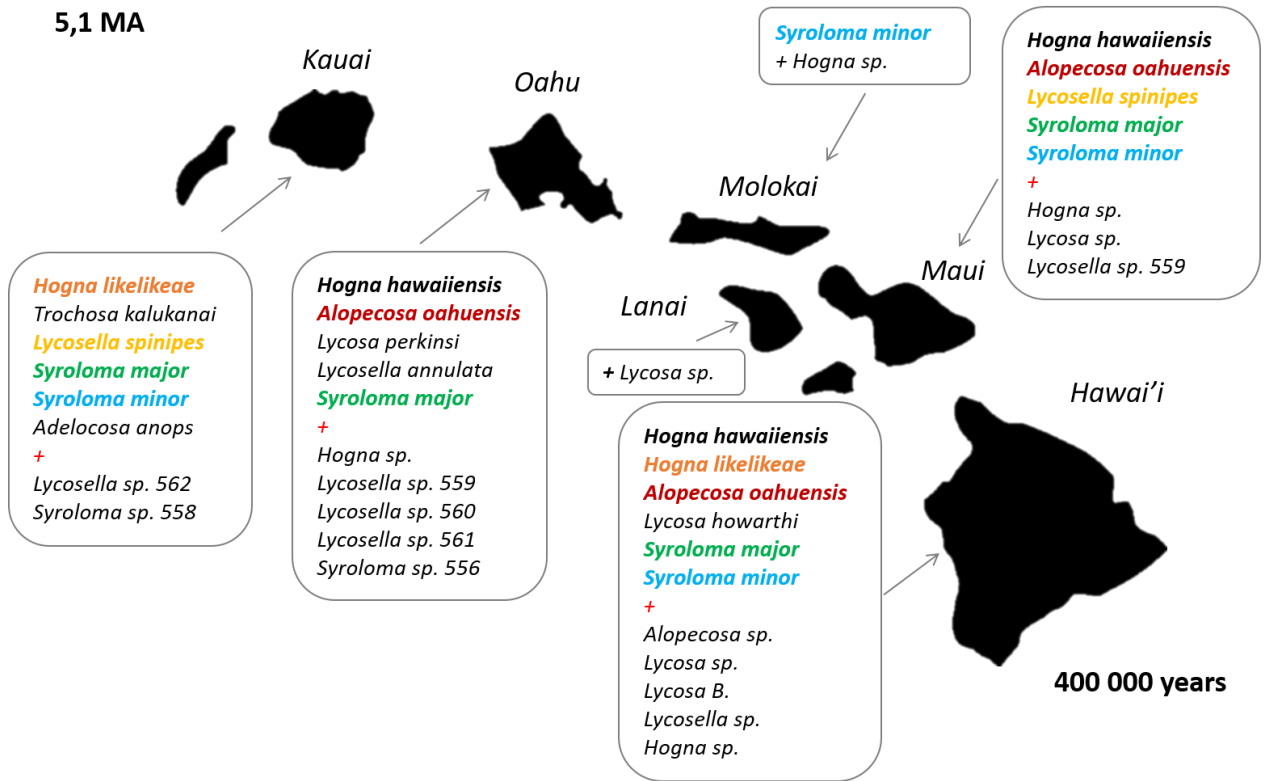


Figure S1: Map of the islands of Hawaii showing the known repartition of the species described to date

Table S1: Details about the specimens sequenced in this study.. *: samples duplicated during PCR, Det.: determination, Elev.: elevation.

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
B76-1 *	-	-	female	Hawaii	Gardner Pinnacles	-	-	-	-	-	1971	Ken Norris	Bishop Museum
Hahua1	-	-	juv	Hawaii	Hawaii	Hualalai	Kealakekua Ranch cave	Cave	-	1310	1972	J. Jacobi, F.G. Howarth	Bishop Museum
HaKi1	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Kilauea	Kaumana Cave	Cave	N19.487° W155.049°	400	2016	Jesse Eiben - Kyle Davis	Bishop Museum
HaKi2	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi3	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi4	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi5	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi6	-	-	juv	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu	Lava flow	N19.36339° W155.21431°	950	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaKi7	Alopecosa ?	sp1	juv	Hawaii	Hawaii	Kilauea	Volcanoes Park (Napau Crater Trail)	Forest	N19.370064° W155.213422°	980	2015	Andy Rominger	Field collection
HaKi8	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi9	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi10	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi11	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi12	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi13	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi14	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum

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HaKi15	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi16	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi17	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi18	-	-	male	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi19	-	-	female	Hawaii	Hawaii	Kilauea	Havo	-	-	2400	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi20 *	-	-	female	Hawaii	Hawaii	Kilauea	Ainahou	-	-	975	1974	W.P. Mull	Bishop Museum
HaKi21 *	-	-	juv	Hawaii	Hawaii	Kilauea	Kilauea Iki Center	Under rock	-	1097	1977	W.P. Mull	Bishop Museum
HaKi22 *	-	-	male	Hawaii	Hawaii	Kilauea	Havo, Mauna Ulu flow	-	-	900	1980	-	Bishop Museum
HaKi23	-	-	female	Hawaii	Hawaii	Kilauea	Puna Kalapana	-	-	304	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi24	-	-	female	Hawaii	Hawaii	Kilauea	Puna Kalapana	-	-	304	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi25	-	-	juv	Hawaii	Hawaii	Kilauea	Puna Kalapana	-	-	304	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaKi26 *	-	-	juv	Hawaii	Hawaii	Kilauea	Kazumura cave	Cave	-	-	1971	F.G. Howarth	Bishop Museum
HaKi27 *	-	-	juv	Hawaii	Hawaii	Kilauea	Kazumura cave	Cave	-	-	1971	F.G. Howarth	Bishop Museum
HaMK1	-	-	juv	Hawaii	Hawaii	Mauna Kea	Visitor Center	-	N19.75616583° W155.4589439°	2800	2016	Julien Pétillon	Field collection
HaMK2	-	-	female	Hawaii	Hawaii	Mauna Kea	Trail from the Mauna kea Visitor Center	Alpine Stone Desert	N19.75616583° W155.4589439°	2800	2016	Julien Pétillon	Field collection
HaMK3	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Kea	Mauna Kea	Alpine Stone Desert	N19.79972° W155.45651°	3775	2014	Jesse Eiben	Paul Blanko
HaMK4	-	-	female	Hawaii	Hawaii	Mauna Kea	Hale Pohaku	-	N19.82189° W155.46895°	4000	2015	Jesse Eiben	Field collection
HaMK5	cf. Alopecosa	sp1	male	Hawaii	Hawaii	Mauna Kea	Mauna Kea	Alpine Stone Desert	N19.82550° W155.47514°	4168	2014	Jesse Eiben	Field collection

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HaMK6	-	-	juv	Hawaii	Hawaii	Mauna Kea	Hale Pohaku	-	N19.81945° W155.46454°	4000	2015	Jesse Eiben	Field collection
HaMK7	Lycosa	sp 1	male	Hawaii	Hawaii	Mauna Kea	Hau Oki	Alpine Stone Desert	-	-	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK8	Lycosa	sp 1'	male	Hawaii	Hawaii	Mauna Kea	Hau Oki	Alpine Stone Desert	N19.82190° W155.46875°	-	2015	Jesse Eiben	Field collection
HaMK9	Lycosa	sp B	female	Hawaii	Hawaii	Mauna Kea	Hau Oki	Alpine Stone Desert	-	-	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK10	Lycosa	sp	male	Hawaii	Hawaii	Mauna Kea	TMT	Alpine Stone Desert	-	-	2018	Jesse Eiben	Field collection
HaMK11	Lycosa	sp 1'	male	Hawaii	Hawaii	Mauna Kea	TMT	Alpine Stone Desert	-	-	2018	Jesse Eiben	Field collection
HaMK12	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	North VLBA	Alpine Stone Desert	-	-	2016	Jesse Eiben - Julien Pétilion	Field collection
HaMK13	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	-	3700	2018	Jesse Eiben	Field collection
HaMK14	Lycosa	Lycosa sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2016	Jesse Eiben - H. Stever	Field collection
HaMK15	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2018	Jesse Eiben	Field collection
HaMK16	Lycosa	sp B	female	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK17b	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2018	Jesse Eiben	Field collection
HaMK18	Lycosa	sp A	female	Hawaii	Hawaii	Mauna Kea	South VLBA	Alpine Stone Desert	N19.80021° W155.45650°	3700	2016	Jesse Eiben	Field collection
HaMK19	Lycosa	sp A	female	Hawaii	Hawaii	Mauna Kea	VLBA	Alpine Stone Desert	-	-	2016	Jesse Eiben - J. Kirkpatrick	Field collection
HaMK20	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	Poi Bowl	Alpine Stone Desert	N19.82354° W155.47536°	4000	2016	Jesse Eiben - Julien Pétilion - H. Stever	Field collection
HaMK21	Lycosa	sp	juv	Hawaii	Hawaii	Mauna Kea	Poi Bowl	Alpine Stone Desert	N19.82354° W155.47536°	4000	2016	Jessen Eiben	Field collection

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HaMK22	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1994	Paul Blanko	Paul Blanko
HaMK23	cf. Alopecosa	sp1	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1994	Paul Blanko	Paul Blanko
HaMK24 *	cf. Alopecosa	sp3	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1992	Paul Blanko	Paul Blanko
HaMK25	cf. Alopecosa	sp3	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1995	Paul Blanko	Paul Blanko
HaMK26	cf. Alopecosa	sp3	-	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1995	Paul Blanko	Paul Blanko
HaMK27 *	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	6/14/1905	Paul Blanko	Paul Blanko
HaMK28	cf. Alopecosa	sp3?	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1993	Paul Blanko	Paul Blanko
HaMK29	-	-	-	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1993	Paul Blanko	Paul Blanko
HaMK30	-	-	-	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8131980666914° W155.60946959632642°	2000	1993	Paul Blanko	Paul Blanko
HaMK31	cf. Alopecosa	sp3?	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK32	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK33	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK34	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK35	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko
HaMK36	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.801815821972056° W155.57058843616934°	2500	1995	Paul Blanko	Paul Blanko

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
HaMK37	cf. Alopecosa	sp3	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8285373612424 68° W155.571056349430 36°	2500	1993	Paul Blanko	Paul Blanko
HaMK38 *	cf. Alopecosa	sp1?	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1992	Paul Blanko	Paul Blanko
HaMK39	cf. Alopecosa	sp3	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1995	Paul Blanko	Paul Blanko
HaMK40	-	-	female	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1995	Paul Blanko	Paul Blanko
HaMK41	-	-	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	N19.8264856877353 1° W155.557368839565 64°	3000	1995	Paul Blanko	Paul Blanko
HaMK42 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK43 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK44 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK45 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK46	-	-	juv	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK47 *	-	-	male	Hawaii	Hawaii	Mauna Kea	western slope of Mauna Kea	Woodland	-	-	1990	Paul Blanko	Paul Blanko
HaMK48	Lycosa	Lycosa B	male	Hawaii	Hawaii	Mauna Kea	Pu'u Huluhulu	-	-	-	1995	-	Bishop Museum
HaMK49	-	-	female	Hawaii	Hawaii	Mauna Kea	Pohakuloa	-	-	-	1992	Gordon	Bishop Museum
HaMK50	-	-	female	Hawaii	Hawaii	Mauna Kea	Bobcat trail, Pohakuloa training area	-	-	1676	1995	Howarth	Bishop Museum
HaMK51	-	-	female	Hawaii	Hawaii	Mauna Kea	Bobcat trail, Pohakuloa training area	-	-	1676	1995	Howarth	Bishop Museum
HaMK52	Lycosa	Lycosa sp a	juv	Hawaii	Hawaii	Mauna Kea	Mauna Kea Forest Reserve	-	19°47'N, 155°36'W	1880	2002	P. Krushelnyc ky coll.	Bishop Museum

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HaMK53	-	-	female	Hawaii	Hawaii	Mauna Kea	Pu'u Huluhulu	-	-	2040	2003	-	Bishop Museum
HaMK54	-	-	juv	Hawaii	Hawaii	Mauna Kea	Pu'u Huluhulu	-	-	2040	2003	-	Bishop Museum
HaML1*	Lycosa	cf Lycosa howarthi (no eye)	female	Hawaii	Hawaii	Mauna Loa	Kula Kai Caverns	Cave	N19.11917° W155.77645°	900	-	Asa Aue, F. Stone	Essig Museum
HaML2	cf. Alopecosa	sp2	female	Hawaii	Hawaii	Mauna Loa	Stainback highway	Forest	N19.57418° W155.21587°	978	2015	Andy Rominger	Field collection
HaML3	-	-	male	Hawaii	Hawaii	Mauna Loa	Pu'u O'o	Lava flow	N19.67174° W155.34570	1600	2016	Julien Pétillon - Jesse Eiben	Field collection
HaML4	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.47585° W155.36391°	1750	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML5	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.686392° W155.465047°	2000	2012	Jesse Eiben	Field collection
HaML6	cf. Alopecosa	sp1	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.686392° W155.465047°	2000	2012	Jesse Eiben	Field collection
HaML7	-	-	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.68696° W155.46407°	2000	2016	Jesse Eiben - Julien Pétillon - Heather Stever	Field collection
HaML8	-	-	juv	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu	Kipuka	N19.68696° W155.46407°	2000	2016	Jesse Eiben - Jorden Zarders	Field collection
HaML9	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.49270° W155.38550°	2000	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML10	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.49270° W155.38550°	2000	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML11	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Access Road	Lava flow	N19.49270° W155.38550°	2000	2016	Pétillon J, E, E, A, K, Y-D	Field collection
HaML15	-	-	-	Hawaii	Hawaii	Mauna Loa	Pu'u Huluhulu saddle road	-	N19.411324° W155.275054°	2011	2016	Jesse Eiben	Field collection
HaML16	-	-	juv	Hawaii	Hawaii	Mauna Loa	Kau Forest Reserve	-	-	1524	2004	S. Benjamin	Essig Museum
HaML17 *	-	-	male	Hawaii	Hawaii	Mauna Loa	Volcano Hongo Store Cave	-	-	-	1971	F.G. Howarth, J. Jacobi	Bishop Museum
HaML18 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Bird Park Cave, kipuka Puauulu, Mauna Loa	-	-	1140	1971	F.G. Howarth	Bishop Museum

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HaML19 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Bird Park Cave, kipuka Puauulu, Mauna Loa	-	-	1140	1971	F.G. Howarth	Bishop Museum
HaML20 *	-	-	female	Hawaii	Hawaii	Mauna Loa	E slope of Mauna Loa	-	-	1220	1971	-	Bishop Museum
HaML21 *	-	-	male	Hawaii	Hawaii	Mauna Loa	Mauna Loa, east slope, treemold area	-	-	1220	1971	J. Jacobi	Bishop Museum
HaML22 *	Lycosa	Lycosa oahuensis (Gertsch det.)	female	Hawaii	Hawaii	Mauna Loa	Havo, Strip Road	-	-	1463	1974	W.P. Mull	Bishop Museum
HaML23	-	-	male	Hawaii	Hawaii	Mauna Loa	Havo	-	-	1500	1998	F. Howarth, T.I. Léon, T.C. Lebeck	Bishop Museum
HaML24	-	-	female	Hawaii	Hawaii	Mauna Loa	Havo, Mauna Loa strip road	-	-	1584	-	W. Gagné, F. Howarth	Bishop Museum
HaML25 *	-	-	female	Hawaii	Hawaii	Mauna Loa	Power Line Road	-	-	1706	1978	W.P. Mull	Bishop Museum
HaML26 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa	-	-	3048	1980	D. Boyton	Bishop Museum
HaML27 *	-	-	juv	Hawaii	Hawaii	Mauna Loa	Mauna Loa Summit, near 1949 cone (1/4 mile)	Lava flow	-	4053	1980	Richard P.	Bishop Museum
HaML28	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina, Happy Hobbit	Cave	-	-	2015	ME Slay, C Slay, ML Porter	Field collection
HaML29	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Akea Ka Mai	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML30	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Akea Ka Mai	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML31	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Xanadu	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML32	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Xanadu	Cave	-	-	2016	ME Slay, C Slay, ML Porter	Field collection
HaML34	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Kula Kai; Chocolate factory	Cave	-	-	2017	ML Porter, SA Engel, AS Engel, P Bosted	Field collection
HaML35	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Kula Kai; Chocolate factory	Cave	-	-	2017	ML Porter, SA Engel, AS Engel, P Bosted	Field collection

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HaML36	Lycosa	Lycosa howarthi	male	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Kula Kai; Chocolate factory	Cave	-	-	2017	ML Porter, SA Engel, AS Engel, P Bosted	Field collection
HaML37	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	ML Porter, AG Hudson, V Hackell, T Gracinin, S Engel	Field collection
HaML39	Lycosa	Lycosa howarthi	-	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Maelstrom	Cave	-	-	2017	CAM Slay, AS Engel, V Hackell, ML Porter, ME Slay, SA Engel	Field collection
HaML40	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Sea reef	Cave	-	-	2018	B Chong, A Hudson, ML Porter, R Thomson	Field collection
HaML41	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	B Chong, A Hudson, ML Porter, R Thomson	Field collection
HaML42	Lycosa	Lycosa howarthi	juv	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	M Slay, Scott Engel, A Katz, S Taylor	Field collection
HaML43	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Cordwinder Natural Bridge Downslope (station 41-43)	Cave	-	-	2018	A Engel, S Engel, J Jacoby, S Taylor	Field collection
HaML44	Lycosa	Lycosa howarthi	female	Hawaii	Hawaii	Mauna Loa	Kipuka Kanohina; Eli's Menehune entrance	Cave	-	-	2018	S Engel, J Jacoby, S Taylor	Field collection
Kauai1	-	-	male	Hawaii	Kauai	-	Nu'alolo trail - Na Pali Kona	Under dirt clump of side of trail	N22.08716° W159.41440°	800	2016	-	Field collection
Kauai2	-	-	juv	Hawaii	Kauai	Kokee State Park	Nualolo trail	-	-	1000	2000	Arnedo, Hormiga & Agnarsson	Essig Museum
Kauai3	-	-	juv	Hawaii	Kauai	Wai'alaie Camp	Camp	-	-	1100	2000	Arnedo, Hormiga & Agnarsson	Essig Museum

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Kauai4	-	-	juv	Hawaii	Kauai	Wai'alaie Camp	Wai'alaie Camp	-	-	1100	2000	Arnedo, Hormiga & Agnarsson	Essig Museum
Kauai5	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee	-	-	1158	2004	Montgomery S.L.	Essig Museum
Kauai6	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee	-	-	1158	2004	Montgomery S.L.	Essig Museum
Kauai7 *	-	-	female	Hawaii	Kauai	Kiahuna	Kiahuna	-	-	-	1979	-	Bishop Museum
Kauai8 *	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee	Woodland	-	-	1963	-	Bishop Museum
Kauai9 *	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee Park	Woodland	-	-	1964	T. Suman	Bishop Museum
Kauai10 *	-	-	juv	Hawaii	Kauai	Koikee State Park	Koikee State Park	-	-	1140	1973	F.G. Howarth	Bishop Museum
Kauai11 *	Adelocosa	Adelocosa anops	female	Hawaii	Kauai	Koloa, Koloa Cave#2	Koloa, Koloa Cave#2	Cave	-	-	1971	F.G. Howarth	Bishop Museum
Kauai12 *	-	-	juv	Hawaii	Kauai	Koloa, Koloa Cave#2	Koloa, Koloa Cave#2	Cave	-	-	1971	F.G. Howarth	Bishop Museum
Kauai13 *	-	-	female	Hawaii	Kauai	Koloa, Koloa Cave#2	Koloa, Koloa Cave#2	Cave	-	-	1971	F.G. Howarth	Bishop Museum
Kauai14	Hogna	Hogna sp.	male	Hawaii	Kauai	Lihue airport	Lihue airport	-	-	-	1993	Mike Linnell + Dean Jamieson	Bishop Museum
Kauai15	Hogna	-	juv	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai16	Hogna	-	juv	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai17	Hogna	-	male	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai18	Hogna	-	female	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Kauai19	Hogna	-	juv	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Kauai20	Hogna	-	female	Hawaii	Kauai	Waiamea	Waiamea Canyon SP, Iliau nature trail	Bush	22°03'6.91"N 159°39'32.11"W	904	2018	Natalie R. Graham	Bishop Museum
Lanai1 *	Lycosa	Lycosa 1	male	Hawaii	Lanai	Pamoi	Pamoi	On loess	-	457	1973	S.L. Montgomery	Bishop Museum
Lays2 *	Alopecosa	Lycosa oahuensis (Gertsch det.)	juv	Hawaii	Laysan	-	-	Dead albatros	-	-	1959	-	Bishop Museum
Lays3 *	-	-	juv	Hawaii	Laysan	At campsit e	At campsite	-	-	-	1987	Marie Maie (?)	Bishop Museum
Lycoannu1 *	Lycosella	Lycosella annulata	juv	Hawaii	Oahu	-	Honolulu	-	-	-	-	Perkins	MNHN
Lycosp1 *	Lycosella	Lycosella sp	juv	Hawaii	-	-	-	-	-	-	-	Perkins	MNHN
Lycospini1 *	Lycosella	Lycosella spinipes	juv	Hawaii	Maui	-	Haleakala	-	-	-	-	Perkins	MNHN
Maui1	-	-	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui2	-	-	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui3	-	-	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui4	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui5	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui6	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui7	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui8	-	-	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Crater	N20.44000° W156.14000°	2800	2006	P. Kruselnycky	Essig Museum
Maui9	-	-	female	Hawaii	Maui	Haleakala	East Maui, Waikau trail, Haleakala Nat. Park	-	-	1980	1996	Howarth	Bishop Museum
Maui10 *	-	-	juv	Hawaii	Maui	Haleakala	East Maui, Haleakala Nat. Park, Puu Laie	Bush	-	2050	1976	F.G. Howarth	Bishop Museum

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Maui11 *	-	-	male	Hawaii	Maui	Haleakala	East Maui, Haleakala Nat. Park	-	-	3000	1980	W.C. Gagné	Bishop Museum
Maui12 *	-	-	female	Hawaii	Maui	Haleakala	Rainforest	-	-	-	1980	R. Warshauer	Bishop Museum
Maui13 *	Lycosella	Lycosella imm.	juv	Hawaii	Maui	Haleakala	Haleakala Nat. Park	Forest	20°44'N, 156°14'W	1859	1981	W.C. Gagné	Bishop Museum
Maui14	Lycosa	Lycosa sp	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	-	20°44'N, 156°14'W	2800	2003	P. Krushelnicky coll.	Bishop Museum
Maui15	-	-	male	Hawaii	Maui	Haleakala	Haleakala Nat. Park	-	20°44'N, 156°14'W	2800	2003	P. Krushelnicky coll.	Bishop Museum
Maui16 *	-	-	male	Hawaii	Maui	Haleakala	East Maui, Waikau trail, Haleakala Nat. Park	-	-	2000	1976	F.G. Howarth, R.C.A. Rice	Bishop Museum
Maui17 *	-	-	male	Hawaii	Maui	Haleakala	East Maui, Haleakala Nat., Silverwood	-	-	-	1975	F.G. Howarth	Bishop Museum
Maui18 *	-	-	male	Hawaii	Maui	Haleakala	East Maui, Haleakala Nat. Park	-	-	3000	1975	W.C. Gagné	Bishop Museum
MoWe0-1	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-10	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-11	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-2	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-5	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-7	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe0-8	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.17460° W157.24843°	0	2016	J. Pétillon	Field collection
MoWe1-12	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
MoWe1-15	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-17	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-19	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-2	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-20	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe1-8	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14772° W157.11333°	150	2016	J. Pétillon	Field collection
MoWe3-1	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-10	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-12	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-14	Hogna	-	female	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-2	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-4	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
MoWe3-5	Hogna	-	juv	Hawaii	Molokai	West	MaunaLoa Highway	Ruderal	N21.14761° W157.14973°	300	2016	J. Pétillon	Field collection
NCal8Brad*	Bradystichus	Bradystichus crispatus	female	New Caledonia	New Caledonia	-	29 a Mt. Mé Ori, pente SE	Forest	165°40'22"E 21°32'18"S	530	1987	A & S Tillier	MNHN
Neck1*	-	-	juv	Hawaii	Necker	Hawaii Isl. (?)	Hawaii Isl. (?)	-	-	-	1982	P. Conant	Bishop Museum
Neck2*	-	-	female	Hawaii	Necker	Hawaii Isl. (?)	Hawaii Isl. (?)	-	-	-	1982	P. Conant	Bishop Museum
Neck3*	-	-	male	Hawaii	Necker	Hawaii Isl. (?)	Hawaii Isl. (?)	-	-	-	1982	P. Conant	Bishop Museum
Nihoa1*	?	-	juv	Hawaii	Nihoa	-	Bottom of Devil's Slide	-	N23.0633° W161.9262°	0	2016	Sheldon Plentovich	Field collection

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Nihoa2	?	-	juv	Hawaii	Nihoa	-	Bottom of Devil's Slide	-	N23.0633° W161.9262°	0	2015	Sheldon Plentovich	Field collection
OaWa1*	-	-	female	Hawaii	Oahu	Waiana'e	Kaena Point	-	-	-	2015	P. Kruselnycky	Bishop Museum
OaWa2*	-	-	female	Hawaii	Oahu	Honolulu	Honolulu, Kalihi, Bishop Museum grounds	Lawn	-	-	1983	F.G. Howarth, W.G. Gagné	Bishop Museum
OaWa3*	Hogna	Hogna crispipes	female	Hawaii	Oahu	Honolulu	Honolulu	-	-	-	1965	A. Miyaharo	Bishop Museum
OaWa4	Hogna	Hogna crispipes	male	Hawaii	Oahu	Kahuluu	Kahuluu	-	-	-	1993	-	Bishop Museum
OaWa5	Hogna	Hogna crispipes	female	Hawaii	Oahu	Kanoeh'e, near Vall. of temples	Kanoeh'e, near Vall. of temples	Outside house	-	-	1993	-	Bishop Museum
OaWa6*	-	-	male	Hawaii	Oahu	Ko'olau	Koolau Mts, Poamoho trail	-	-	700	1977	F.G. Howarth	Bishop Museum
OaWa7*	Hogna	Lycosa hawaiiensis (Roth det.)	female	Hawaii	Oahu	Kunia, Village Park	Kunia, Village Park	-	-	-	1988	F.G. Howarth	Bishop Museum
OaWa8*	-	-	juv	Hawaii	Oahu	Waiana'e	Waiana'e Mts, Kamokuiki Valley	-	-	640	1933	E.H. Bryan Jr	Bishop Museum
OaWa9*	Lycosella	Lycosella sp	juv	Hawaii	Oahu	Waiana'e	Waiana'e Mts, Palikea trail	-	-	650	1980	W.C. Gagné	Bishop Museum
OaWa10*	-	-	juv	Hawaii	Oahu	Waiana'e	Waiana'e Kai Valley	Woodland	-	650	1974	F.G. Howarth, W.G. Gagné	Bishop Museum
OaWa11*	Hogna	Hogna crispipes	male	Hawaii	Oahu	Waipahu	Waipahu	-	-	-	-	Anita Manning	Bishop Museum
OaWa12*	-	-	male	Hawaii	Oahu	Ko'olau	Koolau Mts, Poamoho trail	Under leaves	-	summit	1980	J. Obata	Bishop Museum
OaWa13*	Lycosella	Lycosella sp. (Roth det.)	juv	Hawaii	Oahu	Ko'olau	Tantalus Mt., Ko'olau	Litter in stream bed	-	-	1964	-	Bishop Museum
Rad1	Hogna	Hogna radiata	male	Europe	Europe	-	Dunes Erdeven (56)	Dune	-	-	2004	Cyril Courtial	Gretia
Rad2	Hogna	Hogna radiata	female	Europe	Europe	-	Dunes Erdeven (56)	Dune	-	-	2004	Cyril Courtial	Gretia
Rad3	Hogna	Hogna radiata	female	Europe	Europe	-	Dunes Hoedic (56)	Dune	-	-	2011	Mathieu Lagarde	Gretia
Rad4	Hogna	Hogna radiata	female	Europe	Europe	-	Dunes Guérande (44)	Dune	-	-	2012	Cyril Courtial	Gretia

Code	Genus	Species	Stage	Archipelago or continent	Island	Volcano	Location	Habitat	Coordinates	Elev. (m)	Year of collection	Collector	Collection
Rad6	Hogna	Hogna radiata	male	Europe	Europe	-	Koh Kastell, Belle ile (56)	Lawn	-	-	2000	-	Gretia
Syromin1*	Syroloma	Syroloma minor	male	Hawaii	-	-	-	-	-	-	-	Perkins	MNHN
Syromin2*	Syroloma	Syroloma minor	juv	Hawaii	-	-	-	-	-	-	-	Perkins	MNHN

Table S2: Sizes of the additional amplicons obtained during PCR amplifications and observed on agarose gel

Region	ID	Length (bp)	Size of the multiple amplicons	Average amplicon length
Mitochondrial	COI	365	1000 bp	318
			400 bp	
	CytB	401	450 bp	-
	12S	424	1300 bp	400
			1000 bp	
			900 bp	
800 bp				
16S	371	1000 bp	315	
		400 bp		
Nuclear	18S_A	421	1000 bp	371
			500 bp	
	18S_B	351	900 bp	272
			400 bp	
	28S	363	950 bp	314
			450 bp	
	ITS2	436	1000bp	435
			600 bp	
			500 bp	
	H3	374	650 bp	328
450 bp				
Act5	270	450 bp	226	

18S_A

When doing the phylogenetic reconstruction for the 18S_A (Figure S2), I realized that there were probably two different paralog copies that were selected during the OTU selection. This was shown by two really divergent groups on the tree: one containing 42 samples and the other one 97 samples (apart from the outgroups that contains 7 samples). As previously mentioned, we did not have time to go back to the OTU selection for this preliminary results but we couldn't exclude that much sequences from our analysis. Thus we will here try here to carefully draw up the main patterns given by this phylogeny, considering the two potential copies (referred as upper and lower copy, from their position in the phylogenetic tree).

Overall, the main difference of the phylogeny given by 18S_A compared to the one given by the other loci is its really low resolution with almost all the samples sequenced included in the same bush (in either of the two potential paralogous copies of the gene).

In the group formed by the **upper copy** are found the **cave wolf spiders** and **epigean wolf spiders**. Among the 14 specimens for which we get 18S_A sequences, seven group together in a separated group (blue, bootstrap: 92), and the seven others (names written in red, from Kaumana cave system HaKi1, and from Kipuka Kanohina cave system: HaML1, HaML28, HaML42, HaML32, HaML29, HaML39, HaML37) are in a bush with all the epigean spiders, from the European *Hogna radiata* to wolf spiders found on the islands of Maui, Kauai, Oahu, Nihoa, Hawaii, from low to high elevations (0-4168m).

In the group formed by the **lower copy** are only found epigean wolf spiders from the Hawaiian archipelago. They are separate in three groups including:

- a bush of mainly **low elevations wolf spiders (0-900m) from the islands of Kauai, Oahu and Molokai** and two high elevation spiders from the island of Maui.
- A group of low to medium elevation wolf spiders (300-2500m) from Kilauea and Mauna Kea volcanoes (bootstrap: 99).
- A group of medium to high elevations wolf spiders (1158-4000m) from the Mauna Kea volcano on the island of Hawaii and the island of Kauai (bootstrap: 92).



Figure S2: Maximum likelihood phylogeny of Hawaiian wolf spiders from the 18S_A locus. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support value of the groups of interest are highlighted in red.

18S_B

When doing the phylogenetic reconstruction for the 18S_B (Figure S3), I realized that there were as well probably two different paralog copies that were selected during the OTU selection. This was shown by two divergent groups on the tree: one containing 31 samples and the other one 131 samples. As previously mentioned, we did not have time to go back to the OTU selection for this preliminary results but we couldn't exclude that much sequences from our analysis. Thus we will here try here to carefully draw up the main patterns given by this phylogeny, considering the two potential copies (referred as upper and lower copy, from their position in the phylogenetic tree).

In the group formed by the upper copy are found wolf spiders from the European species *Hogna crispipes* as well as from all the Hawaiian Islands and all the elevations, including two cave wolf spiders (one from Kaumana cave system (HaKi1), one from Kipuka Kanohina cave system (HaML1)). Part of our outgroup wolf spiders (supposedly Artoriinae) group outside of this upper copy.

In the group formed by the lower copy are found two main groups (bootstrap: 97):

- One of epigeal wolf spiders in which we distinguish two sub-groups:
 - A bush of wolf spiders from the islands of Oahu and Hawaii (low to medium elevations: 900-2500m)
 - A group of low elevation (0-904m) wolf spiders from Kauai, Oahu, Nihoa and Molokai (bootstrap: 94).
- One of cave wolf spiders from the island of Hawaii, cave system "Kipuka Kanohina" (bootstrap: 99).



Figure S3: Maximum likelihood phylogeny of Hawaiian wolf spiders from the 18S_B locus. Bootstrap support value (1000 replicates) for each node is depicted on the left side of the node. Bootstrap support value of the groups of interest are highlighted in red.

DISCUSSION GÉNÉRALE ET PERSPECTIVES

Discussion générale: l'habitat joue un rôle dans la diversité des araignées tropicales

Les écosystèmes tropicaux peuvent être considérés comme la "dernière frontière inexploree de la biosphère" où les arthropodes terrestres constituent le groupe le plus diversifié d'eucaryotes. Dans cette thèse de doctorat, nous avons utilisé un ensemble d'approches complémentaires (basées sur les taxons, les traits, les unités évolutives) sur des assemblages d'araignées tropicales dans des systèmes aux habitats contrastés afin de déterminer leurs patterns de diversité et de faire des inférences sur les processus qui en sont localement responsables.

En raison du manque de connaissances sur l'échantillonnage et la diversité des araignées tropicales, nous avons testé et comparé différentes méthodes d'échantillonnage (six) et protocoles standardisés en nous concentrant sur différentes strates de végétation. Nous avons développé une base de données morpho-espèces pour pallier le manque de connaissances taxonomiques. Nous avons étudié un ensemble de traits pour les assemblages d'araignées dans ces environnements, afin de tester leur caractère informatif. Enfin, nous avons déterminé des unités évolutives pour étudier la diversité en appliquant une approche multilocus sur une grande collection d'araignées tropicales, assemblée au cours de cette thèse, pour laquelle les connaissances taxonomiques sont incomplètes et problématiques.

Les principaux résultats de cette thèse sont résumés dans la Figure 1. Ces résultats sont repris et discutés ensemble dans les paragraphes suivants.

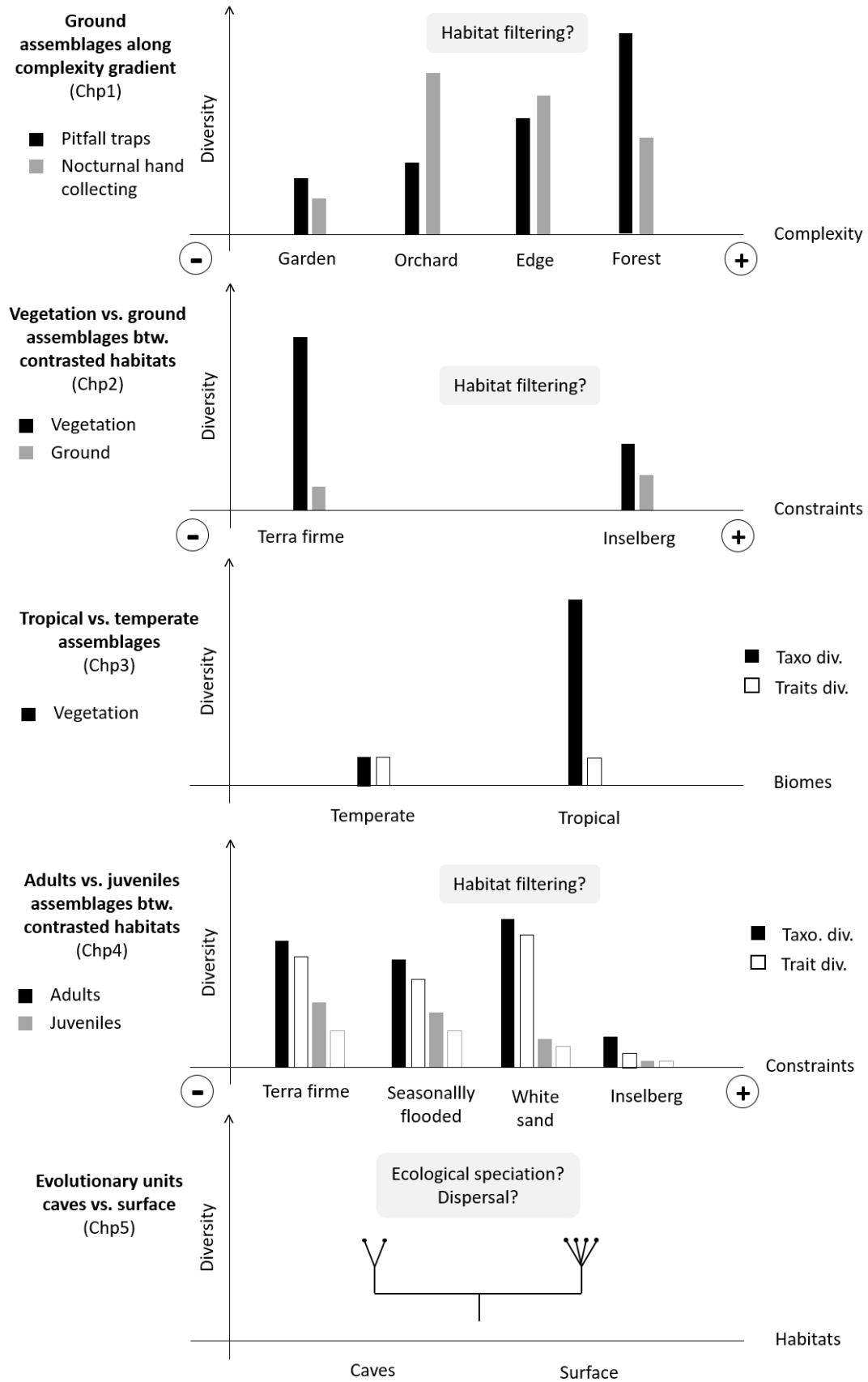


Figure 9: Vue synthétique des résultats obtenus au cours de cette thèse illustrant les différents habitats ainsi que les différents compartiments (e.g. strates, adultes ou juvéniles) étudiés chez les assemblages d'araignées tropicales

En comparant les assemblages d'araignées d'habitats variant en complexité et en contraintes, nous avons montré que ces habitats abritent des assemblages différents avec des diversités de taxons (chapitres 1, 2 et 4) et de traits (chapitres 1 et 4) contrastées. Ces résultats suggèrent l'existence d'un filtrage environnemental sur les assemblages d'araignées tropicales, comme cela a été montré pour les araignées tempérées (e.g. Ridel et al., 2021) et un autre taxon hyperdivers d'arthropodes dans les forêts néotropicales (e.g. les fourmis Fichaux et al., 2019). Cependant, ces patterns ne suivent pas toujours linéairement les gradients d'habitat que nous avons identifiés (chapitres 1 et 4 lorsque les juvéniles sont pris en compte), soulignant la nécessité d'étudier en détail les facteurs qui influencent les assemblages.

La corrélation entre la diversité des taxons et des traits a également été testée au cours de cette thèse de doctorat. A l'échelle locale, la diversité des traits suivait les mêmes tendances que la diversité des taxons entre les habitats contrastés des forêts tropicales (chapitre 4) mais pas entre les habitats plus ouverts et perturbés (chapitre 1, comparaison entre jardin, verger, lisière et forêts). Ces résultats contrastés sont surprenants car la diversité basée sur les traits est connue pour être corrélée à la diversité taxonomique en règle générale, par des effets mathématiques (plantes : Pavoine et al., 2013, araignées : Ridel et al., 2021). A une échelle plus large, les patterns de traits et de diversité taxonomique n'étaient pas corrélés car la différence de diversité taxonomique entre les assemblages tropicaux et tempérés était bien plus élevée que celle de la diversité des traits. Ce résultat fait écho à celui de Cardoso et al. (2011), qui ont montré que la diversité des traits n'était pas toujours plus élevée dans les régions tropicales que dans les régions tempérées, ce qui plaide pour une plus grande redondance des traits dans les assemblages d'araignées tropicales.

En nous concentrant sur les unités évolutives, nous avons montré que les habitats très contrastés (grottes vs surface) abritent des lignées différentes, ce qui suggère un fort filtre environnemental et une spéciation écologique (chapitre 5). En comparant des unités évolutives provenant d'habitats moins contrastés (altitudes et climats différents à la surface), les patterns de diversité dans les unités évolutives étaient moins clairs, suggérant que le filtrage environnemental n'est pas le moteur de la diversité mais que d'autres facteurs, comme la dispersion, influencent la diversité (Chapitre 5).

Les différentes études menées au cours de cette thèse mettent donc en **évidence la forte influence des habitats, et donc du filtre environnemental, sur la diversité des taxons, des traits et des unités évolutives des assemblages d'araignées des forêts tropicales, mais suggèrent également que les taxons et les traits pourraient être pilotés par des facteurs environnementaux différents.**

Perspectives de recherche

L'interconnexion des approches utilisées au cours de cette thèse de doctorat a révélé de nouvelles questions qui devraient être abordées par des recherches futures.

Recherches supplémentaires sur les règles d'assemblage des araignées tropicales

Patterns de diversité contexte et échelle dépendants

Nous avons examiné différents systèmes avec des habitats contrastés : un gradient de complexité jardin-orcherie-bois-riège-forêt (chapitre 1), un gradient de contraintes forêt inondée-forêt inselberg (chapitre 2), forêt sèche-forêt inondée-forêt inselberg, et forêt inondée-forêt sèche-forêt de sable blanc (chapitre 4), ainsi que grotte vs surface (chapitre 5). Les différences de profils de diversité entre ces systèmes (Figure 1) montrent que, compte tenu de nos connaissances sur la taxonomie, les traits et la phylogénie des araignées tropicales, les profils de diversité dépendent du contexte.

L'essai de différentes méthodes d'échantillonnage nous a permis d'étudier la diversité de différentes strates (c'est-à-dire le sol et le sous-étage) et de différents compartiments au sein d'une strate. En comparant la diversité des assemblages d'araignées dans les forêts tropicales inondables et les forêts d'inselbergs, nous avons montré que les assemblages au sol étaient plus diversifiés sur les inselbergs (chapitre 2) alors que les assemblages de sous-étage étaient plus diversifiés dans les forêts tropicales inondables (chapters 2 et 4) (voir figure 1). Russell-Smith & Stork (1994) ont montré que les assemblages de la canopée étaient plus diversifiés sur les inselbergs. En utilisant différentes méthodes d'échantillonnage de la même strate, nous avons montré que les patterns de diversité varient au sein d'une même strate pour le sol (chapters 1 et 2) mais pas pour la végétation (chapters 2 et 4). Au sein d'une même strate, les conditions microclimatiques peuvent varier considérablement et influencer la distribution des espèces (Foelix 2010).

Ces variations des pattern de diversité entre et au sein des strates suggèrent qu'il existe des conditions abiotiques à très petite échelle, constituant des micro-habitats pour les araignées et que ces micro-habitats sont importants dans la structuration de ces assemblages d'araignées tropicales. Un micro-habitat est une petite zone qui diffère de l'habitat environnant en termes de conditions abiotiques telles que la structure et la complexité de la végétation, l'exposition à la lumière ou la température (par exemple, Entling et al. 2007). L'importance des micro-habitats a été constatée dans d'autres assemblages d'araignées (e.g. Jiménez-Valverde & Lobo 2007, Corcuera et al. 2008, Foord et al. 2008, Ziesche & Roth 2008). Il a été suggéré que les assemblages d'araignées peuvent être plus diversifiés sur un plan vertical que sur un plan horizontal (c'est-à-dire qu'entre les habitats, Abraham 1983). Cela confirme ce qui a été trouvé ailleurs sur l'ensemble de l'arthropofaune tropicale, pour laquelle il a été montré que la stratification dans la végétation tropicale ne suit pas les mêmes lois que

dans la végétation tempérée (Basset et al. 1992, 2003), avec notamment des variations plus fines au sein d'une même strate, potentiellement liées aussi au fait que le gradient vertical connu de la végétation tempérée ne se retrouve pas dans la végétation tropicale (Basset et al. 2003). Cependant, les facteurs critiques déterminant cette structuration verticale à petite échelle des assemblages d'araignées tropicales doivent être étudiés en même temps que les facteurs à l'échelle de l'habitat.

Nous notons qu'aucune variabilité des patterns de diversité (diversité taxonomique et composition) n'a été détectée au cours de cette thèse au sein de la strate " sous-bois " (chapitres 2 et 4), ce qui est surprenant car les différentes méthodes d'échantillonnage utilisées ont ciblé différentes strates de celle-ci : la strate inférieure pour le fauchage et la strate supérieure pour le battage (Scharff et al. 2003, Vedel & Lalagüe 2013), ainsi que la strate entière pour le piège Amazonas (Lopes et al. 2019). On peut supposer que la structuration verticale de la végétation de sous-bois pourrait être moins importante pour ces assemblages d'araignées tropicales que pour d'autres assemblages pour lesquels ce paramètre est crucial (par exemple Hansen et al. 2016, Gallé et al. 2017). Cependant, le manque de variation que nous avons observé pourrait également être lié à une structuration plus fine de cette strate de végétation (Basset et al. 2003).

En étudiant les unités phylogénétiques des araignées-loups hawaïennes, nous avons montré que les lignées d'araignées-loups des cavernes pouvaient également être influencées par des variations à petite échelle qui pourraient être limitées par l'environnement, les ressources ou la dispersion (Chapitre 5). La ségrégation trophique (Arnedo et al. 2007) et l'influence des microhabitats (Gillespie et al. 1997, Eberle et al. 2018) sont connues pour jouer un rôle dans la diversification des araignées et doivent être étudiées pour ces araignées-loups.

La variation de la diversité à fine échelle (microhabitats) que nous avons mise en évidence dans cette thèse de doctorat, couplée à la présence de nombreux singletons et à la stratification différente des habitats tropicaux et à la distribution plus fine des assemblages d'arthropodes en leur sein (Basset et al. 1992, 2003) nous amène à nous interroger sur les patterns d'agrégation des araignées en milieu tropical. Coddington et al. (2009) ont examiné les raisons possibles de la surreprésentation des espèces rares ("singletons") dans les assemblages tropicaux et ont conclu que cela est dû à un sous-échantillonnage. Cependant, il est également possible que les faunes d'araignées tropicales suivent différents patterns d'agrégation (Chao et al. 2009, Coddington et al. 2009) qui, selon nous, devraient être étudiés dans les recherches futures afin de comprendre pleinement les règles des assemblages d'araignées tropicales. Nous proposons également que les recherches futures traitent des singletons en examinant si leur rareté basée sur l'abondance est également récupérée en examinant leur statut de rareté basé sur leurs traits et leur phylogénie, c'est-à-dire en évaluant leur originalité de trait et leur originalité phylogénétique (voir Kondratyeva et al. 2019).

Facteurs environnementaux à l'origine des diversités

Les patterns de diversité dépendant du contexte et de l'échelle, ainsi que le fait que les diversités taxonomiques et de traits ne sont pas toujours corrélées (et peuvent donc être déterminées par différents facteurs environnementaux), soulignent la nécessité de tester quels facteurs environnementaux déterminent le filtrage d'habitat à ces différentes échelles et pour les différentes composantes de la diversité. Il existe une importante littérature sur les facteurs qui déterminent les assemblages d'araignées que nous avons commencé à examiner dans ce sens (Entling et al. 2007, Overgaard et al. 2011, Prenter et al. 2012, Hansen, Hansen, Bowden, Normand, et al. 2016, Ameline et al. 2018), et certains comme la structure de la végétation, l'altitude et les inondations seront évalués dans le travail à venir sur les données du chapitre 4.

Repenser l'échantillonnage en milieu tropical : la nécessité d'utiliser un ensemble de méthodes d'échantillonnage dans des protocoles standardisés

En testant plusieurs méthodes d'échantillonnage couramment utilisées chez les araignées (tempérées) et des paramètres connus pour influencer les assemblages (par exemple le jour vs la nuit), nous avons montré que nos connaissances sur l'utilisation des méthodes d'échantillonnage en tempéré ne sont pas généralisables aux assemblages tropicaux, même en appliquant des protocoles standardisés (Chapitres 1 et 2). En effet, les intensités d'échantillonnage sont insuffisantes pour avoir une vision complète de la diversité (Chapitres 1, 2, 3 et 4), les méthodes censées échantillonner les mêmes assemblages montrent des efficacités différentes, échantillonnent des assemblages différents (pour le sol) et détectent des patterns de diversité différents (Chapitres 1 et 2).

En comparant les assemblages d'araignées collectés par des méthodes connues pour cibler les mêmes strates, nous avons démontré que ces différentes méthodes (1) collectent des assemblages différents, en termes de diversité et de composition taxonomique, (2) avec des patterns de diversité taxonomique différents entre les habitats (Chapitres 1 et 2). Nous avons également montré que la prise en compte de la diversité des traits dans l'évaluation de l'efficacité des méthodes d'échantillonnage permet de détecter les méthodes qui collectent une plus grande diversité fonctionnelle (liée aux différents assemblages ciblés par ces méthodes) (Chapitre 1). De plus, une méthode récemment développée (i.e. Amazonas trap, Chapitre 4) ciblant la couche arbustive de la végétation de " sous-bois ", collecte des assemblages dont les patterns de diversité taxonomique et de traits semblent similaires à ceux d'autres méthodes plus connues et utilisées (i.e. battage et balayage, Chapitre 2). Pour caractériser et comparer les assemblages de différents habitats et comprendre les facteurs qui les déterminent, il est donc nécessaire d'utiliser plusieurs méthodes qui échantillonnent a priori la même strate selon des protocoles quasi-optimaux (sensu Malumbres-Olarte et al., 2017) : qui sont standardisés mais qui ne sont pas optimisés pour un seul habitat.

La conception d'un protocole d'échantillonnage universel pour les forêts tropicales est un objectif poursuivi depuis longtemps (Coddington et al. 1991) mais qui ne peut pas encore être atteint en raison du manque de données (Malumbres-Olarte et al. 2017). Aussi, il est

nécessaire de continuer à appliquer et à tester des méthodes et des protocoles d'échantillonnage dans différentes régions tropicales du globe pour accumuler des données, tant sur la diversité taxonomique que sur la diversité des traits collectés par ces méthodes.

En outre, nous considérons que de nouvelles méthodes statistiques pour comparer les diversités en utilisant des approches standardisées basées sur la complétude de l'échantillonnage (Chao et al. 2014, 2021, Hsieh et al. 2016) sont indispensables en raison du sous-échantillonnage de l'assemblage des araignées tropicales (environ 33%, Coddington et al. 2009). Ces méthodes nous semblent une aubaine pour, à l'avenir, réanalyser les données des études précédemment publiées sur la diversité des araignées tropicales et tirer des conclusions sur l'efficacité des méthodes d'échantillonnage.

Importance de la taxonomie

Les difficultés causées par l'absence d'espèces décrites ou par des descriptions douteuses, que ce soit pour l'étude de la diversité taxonomique (chapitres 1, 2, 3, 4) ou pour l'étude des unités évolutives (chapitre 5), nous rappellent l'importance d'une taxonomie claire et à jour dans la compréhension des modèles de diversité. L'utilisation de la parataxonomie montre ses limites, dans des cas comme celui des araignées-loups hawaïennes (chapitre 5) où le conservatisme morphologique est tel que les frontières des espèces (si elles existent) sont impossibles à déterminer sur une base morphologique sans une révision complète des membres de la lignée et des informations sur la diversité évolutive.

La diversité des araignées tropicales est telle que la tâche de description des espèces est monstrueuse et semble insurmontable, malgré l'activité des arachnologues taxonomistes (Agnarsson et al. 2013, Jäger et al. 2021), en raison du contexte actuel dans lequel la taxonomie est peu attrayante et non financée (Engel et al. 2021). Dans le contexte d'un groupe hyperdiversifié comme les araignées tropicales, il nous semble donc que les méthodes moléculaires pourraient être une aide particulièrement adaptée à la délimitation des espèces. Ainsi, nous encourageons les futures recherches sur les araignées tropicales à moderniser leurs pratiques de collecte afin d'être en mesure d'utiliser des outils moléculaires (NGS, i.e. RADtags) pour délimiter et décrire les espèces inconnues rencontrées (Ivanov et al. 2021, mais voir aussi Courtial et al. soumis, Annexe 4 pour une simple investigation COI) et au mieux appliquer des méthodes génomiques à ces collections (Card et al. 2021). Nous encourageons ces recherches à utiliser également des outils tels que la plateforme portable MinION, qui permet de réaliser le séquençage dans des conditions tropicales isolées (Pomerantz et al. 2018, Krehenwinkel et al. 2019).

Vers le développement d'une approche basée sur les traits adaptée aux écosystèmes tropicaux.

Comme mentionné dans l'introduction et montré dans les différents chapitres de cette thèse (chapitres 1, 3 et 4), les connaissances sur les traits des araignées, et des araignées tropicales en particulier, sont limitées. La création de la World Spider Trait Database devrait permettre d'accumuler plus de connaissances à leur sujet. Cependant, cette base de données n'accepte que les traits des espèces décrites (Lowe et al. 2020, Pekár et al. 2021), ce qui renforce encore l'importance et l'urgence de décrire les espèces d'araignées tropicales.

Dans le chapitre 4, nous avons mesuré un ensemble de traits dont les corrélations avec les variables environnementales nous permettront de les relier à des facteurs potentiellement déterminants des assemblages. Cette exploration est laborieuse mais nécessaire (e.g. Wong & Carmona 2021) et permettra un gain qualitatif dans l'étude des traits dans les assemblages tropicaux.

Enfin, en raison du fort sous-échantillonnage inhérent aux assemblages d'araignées (et d'arthropodes) tropicaux en général (Coddington et al. 2009), dans des conditions d'intensité d'échantillonnage réalisable, les comparaisons de diversité dans les assemblages tropicaux ne sont rigoureuses que si elles tiennent compte de l'exhaustivité de l'échantillonnage (Chao & Jost 2012, Chao et al. 2020). Bien qu'il existe une méthode pour estimer la diversité taxonomique (Chao et al. 2014, Hsieh et al. 2016), elle n'a été développée que récemment pour la diversité des traits (Chao et al. 2021, utilisée au chapitre 4).

Utilisation du NGS pour résoudre des relations évolutives complexes

Résoudre les relations phylogénétiques et l'origine de la radiation des araignées-loups hawaïennes nécessitera (1) un échantillonnage plus complet de l'archipel (surface et grottes) ainsi qu'un échantillonnage du Pacifique et des continents voisins et (2) l'utilisation d'approches pangénomiques. Dans ce sens, des échantillons de tout le Pacifique, provenant de collections de musées, ont été rassemblés et partiellement séquencés au cours de cette thèse. Ils devraient être inclus dans les analyses futures. De plus, un vaste échantillonnage en surface et dans les grottes de l'archipel hawaïen devait être réalisé au cours de cette thèse mais a été retardé en raison de la pandémie de Covid-19. Ce travail de terrain devrait être réalisé au printemps 2022. Une étude supplémentaire sur les espèces cavernicoles est en cours en collaboration avec le Dr Megan Porter et le Dr Rebecca Chong, de l'Université de Hawai'i, Manoa, qui ont récemment soumis une proposition NSF intitulée " Collaborative Research " : BEE : Bridging the space-time continuum to investigate how biodiversity scales across subterranean systems" à laquelle je vais collaborer. En particulier, nous prévoyons de caractériser les caractéristiques anatomiques de la modification des yeux de l'araignée-loup hawaïenne et de faire de la génomique des populations sur les différents systèmes de grottes.

Conclusion

L'interconnexion des approches utilisées au cours de cette thèse de doctorat a révélé l'influence de l'habitat dans les patterns de diversité des taxons, des traits et des unités évolutives des araignées tropicales et par conséquent l'importance du filtrage de l'habitat dans les assemblages d'araignées tropicales. En outre, nous avons montré la nature contextuelle et échelle dépendante des patterns de diversité des araignées tropicales avec des variations des assemblages d'araignées tropicales à une échelle plus fine que celle des habitats. Globalement, cela plaide pour davantage d'études de cas étudiant les patterns de diversité tropicaux à l'échelle des strates, des sous-structures de végétation et des conditions de micro-habitats, pour lesquels nous suggérons des axes de recherche. Nous avons également pu faire des propositions pour améliorer l'échantillonnage des assemblages d'araignées tropicales, ce qui devrait permettre d'obtenir des données comparables pour élaborer, dans un avenir proche, les grandes lignes d'un protocole d'échantillonnage universel pour les forêts tropicales. Aujourd'hui, nous avons la chance de disposer d'outils de partage de données (World Spider Catalog, World Spider Trait Database) ainsi que de nouvelles méthodes d'analyse (statistiques, séquençage), qui nous permettront de combler ce manque de connaissances dans les années à venir. Enfin, ce travail rappelle la nécessité de continuer à développer les connaissances taxonomiques, de continuer à utiliser l'espèce comme unité de base des études en écologie des communautés.

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ARTICLES ANNEXES

ANNEXE.1

Vers l'établissement d'une base de données centralisée sur les traits des araignées

Towards establishment of a centralized spider traits database

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Abstract

A main goal of ecological and evolutionary biology is understanding and predicting interactions between populations and both abiotic and biotic environments, the spatial and temporal variation of these interactions, and the effects on population dynamics and performance. Trait-based approaches can help to model these interactions and generate a comprehensive understanding of ecosystem functioning. A central tool is the collation of databases that include species trait information. Such centralized databases have been set up for a number of organismal groups but is lacking for one of the most important groups of predators in terrestrial ecosystems – spiders. Here we promote the collation of an open spider traits database, integrated into the global Open Traits Network. We explore the current collation of spider data and cover the logistics of setting up a global database, including which traits to include, the source of data, how to input data, database governance, geographic cover, accessibility, quality control and how to make the database sustainable long-term. Finally, we explore the scope of research questions that could be investigated using a global spider traits database.

Key-words: Phenotypic traits, functional diversity, functional ecology, ecosystem functioning, evolutionary ecology, comparative analysis

Introduction

We are living in an age of large-scale assembly of digital information. The generation of large databases across scientific disciplines is now enabling the modeling of natural processes on an unprecedented scale. The development of the world wide web over the last three decades has aided the centralization of collated data and has enabled the storing and sharing of large amounts of data. Biology has truly arrived in the information age with the large-scale digitization of information and its central storage in online databases (e.g., GenBank, BOLD, Dryad). These databases have become the core of many recent research advances.

In ecology and evolutionary biology, the accessibility of large-scale genetic information reaches its true potential when linked with phenotypic and faunistic data. For instance, comparative studies of organismal traits among species or across space, time or habitat types, can reveal general patterns that help to predict changes in biodiversity and ecosystem functioning in a rapidly changing world (Krause et al. 2014; Madin et al. 2016b; Wright et al. 2017; Dudley et al. 2019; Mammola et al. 2019). However, the development of open databases for phenotypic data is lagging far behind. This not only limits progress in the life sciences, but also leads to inefficient duplication and impairs reproducibility of research. Major reasons for the slow and reluctant establishment of trait databases are the perceived difficulty to unify data and to standardize reporting methods. In contrast, for molecular data these challenges have been overcome, facilitating the rapid growth of molecular databases. Furthermore, the inclusion of new molecular data into such central databases is highly promoted. For example, final acceptance of a publication in many scientific journals is contingent on the submission of genetic data to a genetic database (e.g., GenBank).

Compared to genetic data, trait data are much harder to standardize across taxonomic groups due to different terminologies and methods used for their measurement and recording. Therefore, existing trait database projects are taxon-specific and often constrained to specific traits or geographic regions (e.g., Kattge et al. 2011; Homburg et al. 2014; Brun et al. 2017; Madin et al. 2016a; Oliveira et al. 2017; Parr et al. 2017). There are good reasons to continue with the assembly of taxon-specific trait databases as this approach offers the flexibility required to tailor the database to the need of the focus field (e.g., entomology, herpetology, botany, microbiology). The data deposited in different taxon-specific databases could be synthesized into a central node by the identification of common or equivalent traits that can be easily

translated into cross-taxon standards (Gallagher et al. 2020). Examples of such traits already in use in cross-taxon studies are body size, trophic niche, habitat preferences, and metabolic rates.

Hence, the building of taxon-specific trait databases can bring enormous benefits both for the specific field compiling the data (e.g., arachnology) as well as for cross-taxon analyses. Here, we propose to set up a community-based spider trait database (Arachnida: Araneae) and invite submissions of data from the arachnological community.

Spiders are a mega-diverse order of animals, with about 48,400 species currently identified (World Spider Catalog 2020), and one of the most dominant groups of invertebrate predators in terrestrial ecosystems (Turnbull 1973). They thus play a key role in ecosystem function worldwide, such as increasing crop performance by suppressing pest density (Michalko et al. 2019). Spiders are premier subjects to study fundamental biological mechanisms, such as sexual selection (Herberstein et al. 2013), the evolution of sociality (Lubin & Bilde 2007) and extended phenotypes (Blackledge et al. 2009), predator-prey interactions (Pekar & Toft 2015), community assembly (Birkhofer et al. 2017), and migration (Gillespie et al. 2012). They are also in the focus of the applied sciences, such as agro-ecology (pest control) (Uetz et al. 1999; Birkhofer et al. 2016; Michalko et al. 2019), material science (spider silk) (Wolff et al. 2017) and medical science (venom) (King & Hardy 2013).

General database benefits

Trait databases are particularly useful for comparative studies and studies on biodiversity and the function of ecological communities. Traditionally, such research relied on the primary collation of comparative data by laborious measurements in a large number of species and specimens or time-consuming gathering from print-literature. The widespread lack of access to primary or even derived data has not only contributed to the reproducibility crisis of science (Allison et al. 2018) but also led to an unnecessary redundancy in data acquisition, wasting time and money. Only recently has it become a common good scientific practice to make the raw data that underlie a study available to the scientific community. While this enhances transparency, it does not necessarily solve the problem of work redundancy as such datasets that are largely hidden in appendices, electronic supplemental material or on file servers instead of a central repository. The building of a commonly accepted trait database is a solution.

Having open access to a database of relevant trait data not only boosts comparative and ecological studies, but also allows researchers to undertake quick exploratory analyses to generate preliminary data that may be useful for project planning and funding justification in grant applications. Well populated databases also make it possible to detect knowledge gaps or geographical biases, which can be used to identify future areas of research.

Trait databases thus fill an important gap in the digitization and accessibility of biological knowledge and can become a powerful tool when linked with existing taxonomic (World Spider Catalog 2020), semantic (Spider Anatomy Ontology—SPD (Ramirez & Michalik 2019)), molecular (BOLD (Ratnasingham & Hebert 2007), Genbank (Benson et al. 2012), ArachnoServer (Pineda et al. 2018)) and faunistic (e.g., Atlas of the European Arachnids; Atlas of Living Australia; Araneae Spiders of Europe (Nentwig et al. 2020); Global Biodiversity Information Facility—GBIF) resources (See Table. 1 for current databases that include spider traits). Finally, a trait database can also serve as a central data repository to fulfil the requirements of data accessibility.

Table 1.—Examples of existing databases which include data for spiders (overview compiled in January 2020).

Name	Geographic range	Data types	Number of species included	Link
Genbank	Global	DNA sequences	12537	https://www.ncbi.nlm.nih.gov/genbank/
BOLD	Global	DNA barcodes	10552	http://www.boldsystems.org/
British Spider and Harvestman Recording Schemes	Britain	Distribution, ecology, habitat	713	http://srs.britishspiders.org.uk/
Czech spider database	Czech Republic	Distribution, habitat	896	https://www.arachnology.cz/rad/Araneae-1.html
GBIF (Global Biodiversity Information Facility)	Global	Occurrence records	50708	https://www.gbif.org/
World Spider Catalog	Global	Taxonomy, species distribution	48423	https://wsc.nmbe.ch/
ArachnoServer	Global	Toxin sequence, structure and biological activity	100	http://www.arachnoserver.org
Araneae Spiders of Europe	Europe	Distribution, morphology (body length, diagnostic illustrations), habitat	5210	https://araneae.nmbe.ch/
Global Species Database of Salticidae	Global	Distribution, morphology (diagnostic illustrations)	6990	http://www.salticidae.pl/
Jumping spiders (Arachnida: Araneae: Salticidae) of the world	Global	Distribution, morphology (diagnostic illustrations)	6149	https://www.jumping-spiders.com/
Spider Anatomy Ontology (SPD)	Global	Ontology of anatomical terms	NA	http://bioportal.bioontology.org/ontologies/SPD

Benefits of a spider traits database

Setting up a global trait database for spiders will elevate arachnology to the next level of biodiversity digitization: having open and better access to data will bring arachnology together and create stronger collaborative networks able to address a wide range of questions (as explored below). It will make global or large-scale studies possible within a fraction of the time and improve the statistical power of many analyses. A centralized database will also help to identify species' vulnerability and guide conservation decisions (Gonçalves-Souza et al. 2015). It can also help to inform taxonomic decisions since the database acts as a source of information about variability (e.g., geographic and morphological).

Beyond arachnology, a spider trait database will facilitate the inclusion of spiders in global multi-taxa studies and biomonitoring programs. The topical research area of biodiversity-ecosystem functioning relationships often utilizes metrics of functional diversity that are based on traits in crosstaxon studies. The collation of global data will also provide better information for outreach purposes. For example, the database could provide information

about local diversity of spiders, size comparisons or peculiar species that are accessible to local residents. A comprehensive understanding of the functional and ecological diversity of spiders, if adequately published for the general audience, can help to improve the public perception of spiders.

As existing trait database projects are largely family-focused and no such database yet exists for any arthropod order, the arachnological community could lead a frontier project for higher-level animal trait databasing. We think that arachnologists are in an excellent position to swiftly establish a spider trait database due to its outstanding achievement of digitization of all taxonomical literature (Nentwig et al. 2015) and the existence of a digital taxonomic standard, the World Spider Catalog (WSC) (2020), which makes possible the large-scale extraction of basic traits, such as area of distribution or body size (e.g., through text mining approaches), and their automatically updated taxonomic assignment (through a unique LSID identifier).

Logistics of a traits database

Some of the logistics of setting up a trait database require consensus on: trait definitions, the source of data, how to input data, database governance, geographic cover, accessibility, quality control, financial needs, and how to achieve the database's long-term sustainability. Below we propose principles that, in our view, will make a useful framework for a spider trait database.

Definition of traits.—One of the fundamental problems with collating traits in particular is the confusion and debate around the term “traits”, and in particular “functional traits” (Violle et al. 2007; Pey et al. 2014; Moretti et al. 2017; Brousseau et al. 2018; Wong et al. 2019). At their most basic form, all observable and quantifiable characters are traits. While some traits directly imply an ecological function (e.g., ‘habitat preference’ (Rusch et al. 2015)), for basic phenotypic data, such as body shape, the link to function is often not experimentally established and remains hypothetical. Furthermore, to be useful for a wide range of topics beyond functional ecology, a database should be flexible enough to accommodate a diversity of data types. For a spider trait database, we propose that the term ‘trait’ should thus be applied in a broad sense and include all observable and quantifiable characters on the level of individuals, populations or species, irrespective of our current assumptions on their functional role.

For a highly versatile database, we propose the inclusion of the following trait categories: (a) Ecological (e.g., (micro-) habitat preference, hunting mode), (b) Behavioral (e.g., stratum utilization, maternal care), (c) Morphological (e.g., body length, leg length), (d) Physiological (e.g., reproductive rate, resting metabolic rate, thermal limits) and (e) Biomechanical (e.g., running speed, silk strength). In the future, the database may also be expanded to include more categories.

Data types.—Another challenge is that the nature of traits can be diverse: traits can be quantified and described using data that are descriptive (e.g., Latin name of a prey item), categorical (e.g., web-builder, active hunter), ordinal (e.g., small, medium, large), interval (e.g., 1–3, 4–6), ratio (e.g., 10:100; 20:100), discrete (e.g., 1,2,3) or continuous (e.g., 1, 3.5, 7.2). There are many examples where qualitative information is sufficient in order to capture the traits, but problems arise when researchers apply different terminologies, definitions and categorizations for observations or characteristics. While common standards must be identified for each trait to ensure comparability (e.g., fixing units for numerical traits), the versatility of trait input can be maintained by a liberal trait definition with the accurate method (e.g., recording scheme) defined in the meta data, which permits the filtering for comparable data at the analysis stage (Jones et al. 2006). Another solution is to handle differently recorded trait data under separately defined traits.

The use of non-equivalent data types for some traits presents further difficulties. For instance, different authors report phenology, habitat preferences or prey type as binary or in frequencies. Furthermore, the state of some categorical traits might be ambiguous or context dependent. For instance, in many orb-web spiders (Araneidae), the adult males abandon webs, and some long-jawed orb-web spiders (Tetragnathidae) can be both web-building or free hunting. This problem can be solved by recording any categorical trait state as binary with the option to provide a frequency for each character state and a record of the sample size. Some traits are covarying, e.g., body length and leg length. This can be accounted for by linking trait records that are derived from the same object (i.e., specimen, individual or population).

Intraspecific variation.—The impact of intraspecific variation on comparative approaches has been widely demonstrated (Garamszegi & Møller 2010) and has also been recognized in community ecology (Bolnick et al. 2011). Some spider species, such as *Argiope bruennichi* (Scopoli, 1772) (Araneidae) have a wide distribution range and show an enormous variation in phenology, morphology and behavior depending on the geographical location (Krehenwinkel & Tautz 2013; Wolz et al. 2020). In such instances, a single trait record may not be representative for a species. The trait database can provide the opportunity to accommodate multiple records per species and attach relevant information about the record context (such as locality, date and developmental stage) in the metadata.

Taxonomic integrity.—A serious challenge for the maintenance of multi-species datasets is taxonomic changes. Fortunately, with the World Spider Catalog (2020), arachnology has a reliable and maintained source for changing taxonomic information. A key is the assignment of a unique identifier (the Life Species Identifier (LSID)), which is constant and can be used as a link between the spider trait database and the World Spider Catalog to automatically update the taxonomic information in the database. To make any changes traceable, we propose that species names originally used in uploaded datasets must be kept in the metadata.

Database governance and data upload.—The spider trait database will be a community-driven project, created and maintained by a team of 5–10 administrators and a webmaster. To upload data, the contributor must use a template that provides the structure for how the

data and attached metadata are reported. An annotated draft template can be found in the electronic supplemental material of this article (Supplemental materials Online at <http://dx.doi.org/10.1636/JoA-S-20-011.s1>). At this stage, any trait data can be sent to the corresponding authors of this paper using this template for its inclusion into a first version of the spider trait database. The database will be hosted by Masaryk University, Czech Republic, and curated by Stano Pekar's research team and collaborators.

Quality control.—Databases require some degree of curation in order to maintain their integrity. While some of the data checking can be automated (i.e., if all mandatory fields contain information and data types for traits are correct), we think that the content of submissions must be formally crosschecked and approved by an expert before it is published in the database. This may include a quick check, if the uploader is a known expert, if the data are of relevance for the database, if the data are accompanied by a citable publication that described the methods of data acquisition and that there are no obvious errors (e.g., false units and digits). The formation of an editorial board with experts for specific types of traits (e.g., behavior, morphology, habitat) will help to facilitate the described curation task.

Accessibility.—Following the principles of FAIRness and open science (Wilkinson et al. 2016) and facilitating its embedding in the Open Traits Network (Gallagher et al. 2020), we promote open accessibility of the spider trait database. This can be enabled by the use of the creative commons license CC-BY 4.0, which means that anyone will be able to download and use the data for their own research with the appropriate citation of the database.

Author attribution.—Authorship models and citation rules for database usage are matter of dispute at trait database meetings. The reason is that the processing and integration of data from thousands of sources makes it hard to define what makes a significant contribution that merits authorship and who must be named and cited according to the ethical norms of science and the CC-BY license (Gallagher et al. 2020). Here it can be useful to distinguish between the authors of the original data sources (i.e., the publication from which data were extracted to build a comparative dataset) and the authors of the data synthesis (i.e., researchers who collated the comparative data set and/or made the database accessible in a systematic manner). For practical reasons, we propose that only the latter merits authorship of the database.

Following the above standards of reproducibility and traceability, it will be a requirement to cite the original data sources (preferably with a DOI) in the database. However, among the research community there is no consensus about whether original sources of legacy data must be cited in a publication that uses data from the database, and this decision is often left to the users (Gallagher et al. 2020). On the other hand, it is commonly accepted that any outputs derived from the trait database will reference the database (the synthesis). In order to become citable, the database will be released alongside an article in a scientific journal that describes the database. For the spider trait database, it is aimed to publish its formal description in a major Open Access journal. After the release, the database will be continuously updated and

its content expanded. Major changes to its content and the author team will require the occasional publication of a new article under a changed version number of the database.

Additional challenges for a spider traits database

The first major challenge of creating a spider trait database stems from the huge diversity of spiders (48,400 described species and many yet to be discovered), largely preventing arachnologists from gathering traits for all of them. One solution to this problem is to integrate data from related species in the analysis step, in a careful and controlled manner, which is a widespread procedure in comparative analyses of invertebrates (e.g., Madin et al. 2016b).

Second, many ecological studies use “morphospecies”, where species identification is considered too difficult. If species names are lacking, the common standard that makes the data comparable is missing. We argue that the arbitrary definition of morphospecies cannot replace species identification by experts, e.g., by comparison with species descriptions and type material, and we do not promote the inclusion of trait data from morphospecies into the database. However, to avoid the exclusion of data from lesser known taxa, the database will allow the use of genus levels as a common standard (i.e., usage of the genus LSID, if species identities are unknown or yet to be described). It will be encouraged to specify voucher IDs and locations, if present, in the meta data, to enhance the tracing of species identifications.

Potential research that would become feasible with a spider traits database

Metacommunity, macroecology and biogeography.—At its most basic level, a traits database will help answer questions about how traits are geospatially distributed across taxa. Studies on how traits evolve or change at the community level in response to natural and historic change would also be facilitated. Having access to data relating to trait composition and body size will enable researchers to study the macroecological drivers of functional diversity at broad spatial and temporal scales (Cardoso et al. 2011). It will also enable the study of the relative contribution of environmental filtering, dispersal-related processes and competitive exclusion in determining spider assemblages and their functional diversity (Jimenez-Valverde et al. 2010; Carvalho & Cardoso 2014). How the mechanisms of environmental filtering influence community assembly along environmental gradients (e.g., climatic, altitudinal, latitudinal, structural) and by abiotic and biotic disturbances (e.g., floods, fire and biological invasions) can also be investigated by integrating data from the trait database with data from other online resources, such as climatic databases (Carvalho et al. 2020). The integration of vegetation biome data and climatic gradients allows for the testing of the relationship between vegetation, latitude and functional diversity of spider communities. Finally, the effects of urbanization on the expression or evolution of spider traits could be studied on a global scale (Lowe et al. 2018).

Evolution.—To date, trait-based research is a topic largely promoted within macroecology, and less recognized in comparative biology. However, the digitization of traits has

considerable potential for the fields of comparative, evolutionary and systematic biology. By linking phylogenomic data with trait data, fundamental evolutionary questions can be studied on a large taxonomic scale, such as the evolution of body size (Kuntner & Coddington 2019) and the extended phenotypes (Blackledge et al. 2009). It would also be interesting to examine connections between phylogenetic diversity and functional diversity and to test the ‘stable species hierarchy hypothesis’ in spiders, which predicts that trait variation is higher at the interspecific level than at the intraspecific level (Kazakou et al. 2014). Furthermore, testable ideas include whether diversification processes have been accompanied by expansions or shifts in trait space and how the evolution of different traits are correlated.

Ecology and ecosystem functioning.—Trait based research can help to understand how communities and ecosystems work by unraveling the interactions between species and their ecological roles. With a comprehensive spider trait database, it could be feasible to identify which traits are associated with specific habitat types, such as the ones found in caves, deserts or mountain summits. In combination with similar databases of other taxa, the traits affecting ecosystem functioning, those affected by ecosystem processes, and traits that are redundant could be identified. Also, functional traits that have a similar (or complementary) ecological function could be identified. From an applied perspective, understanding which traits contribute to high levels of pest control by spiders (“effect traits”, Rusch et al. 2015) and how this service may be supported by certain management practices (“response traits”, Birkhofer et al. 2014) is an important research field in agriculture and forestry. Questions of niche formation in a competitive setting could be addressed, for instance what are the traits that confer competitive advantages under different circumstances.

Conservation.—The proposed spider trait database can guide conservation decisions. By identifying species that exhibit a unique combination of traits, local conservation can guide efforts targeting these species (Birkhofer et al. 2017). Comparative studies can reveal traits that are associated with species’ extinction risk, resilience or the recolonization of restored areas, for instance using model species’ vulnerability to climate and habitat changes (Chichorro et al. 2019). Future threats to biodiversity from land-use change or intensification could become predictable, if we understood community responses from a trait perspective. Comparing both taxonomic and functional diversity responses to agricultural intensification provides an ideal framework to consider trade-offs and synergies between different conservation goals (Birkhofer et al. 2015). To understand which species are threatened by the pet trade, the database can identify the traits, such as size or color, that make a spider attractive to the buyer.

Outlook

This paper demonstrates how the arachnological community and biologists more broadly would benefit from a global spider traits database. We have discussed the challenges that the development of a comprehensive trait database brings for a megadiverse group such as spiders and have provided possible solutions for each problem. We suggest that establishing

the spider traits database is feasible, but will require major support, endorsement and input by the community. Following a fruitful workshop on 10th February 2019, at the 21st International Congress of Arachnology in Christchurch, New Zealand, an action group has formed that is currently working on the implementation of the principles discussed in this article. The team, led by Stano Pekar, is currently setting up the online database, with the release of a first version planned for the end of 2020. We are requesting both data submissions (using the provided template) and participation in editing, testing and data curation. For questions, suggestions and offers please contact the corresponding authors of this article.

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ANNEXE.2

La base de données World Spider Trait (WST) : un référentiel mondial ouvert et centralisé pour les données sur les traits des araignées

The World Spider Trait database (WST): a centralized global open repository for curated data on spider traits

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Database (2021), 2021, baab064

Abstract

Spiders are a highly diversified group of arthropods which play an important role in terrestrial ecosystems as ubiquitous predators, making them a suitable group to test a variety of eco-evolutionary hypotheses. For this purpose, knowledge of a diverse range of species traits is required. Until now data on spider traits have been scattered across thousands of publications produced for over two centuries and written in diverse languages. To facilitate access to such data we developed an online database for archiving and accessing spider traits at a global scale. The database has been designed to accommodate a great variety of traits (e.g., ecological, behavioural, morphological) measured at individual, species or higher taxonomic levels. Records are accompanied by extensive metadata (e.g., location, method). The database is curated by an expert team, regularly updated and open to any user. A future goal of the growing database is to include all published and unpublished data on spider traits provided by experts worldwide and to facilitate broad cross-taxa assays in functional ecology and comparative biology.

Background & Summary

With almost 50,000 species described to date¹, spiders are among the most diverse orders of terrestrial arthropods². Spiders rank among the most dominant arthropod predators in a huge variety of ecosystems, and therefore provide important ecosystem services, such as biological control^{3,4} and bio-indication⁵. They are also potentially an important source of molecules to be used in new biotechnologies and human medicine^{6,7}. In addition to these uses, spiders provide suitable models to test a breadth of ecological and evolutionary hypotheses⁸⁻¹⁰.

Successful use of spiders for research and environmental assessments is based on knowledge of traits (morphological, ecological, physiological or behavioural characteristics) which characterise responses to environmental conditions and both change and define the effects of spiders on ecosystems functioning¹⁰. Assembling trait values for species in a community is laborious because for some traits and species this information either does not exist or is not easily available as it is hidden in old publications (often not in English), unpublished records, technical reports, or even field notes. Although difficult to access, the data available are extensive, as research on spiders has covered a huge diversity of topics for over 200 years¹¹. Data on spider traits continues to be generated on a daily basis, most of it being used in individual publications or retained in unpublished datasets. Trait data are stored in different places and forms, and most data that originated before the use of personal computers are only available from printed publications. More recently collected data are often stored in digital form in different repositories (from personal computers to data archive servers), but it is often difficult to compile and standardize datasets with different formats, and completeness of metadata, necessary for leveraging data for common purposes as pointed out in the concept of Essential Biodiversity Variables^{12,13}.

A single database that accommodates all trait data would enable scientists to investigate spiders more effectively and to perform large-scale comparative analyses¹⁴⁻²⁰. A trait-based approach has the advantage that some investigations (e.g. bio-indication) can be performed even when the taxonomic identity is missing or inaccurate (using morphospecies, for example)²¹. Using trait, instead of taxonomic information, also allows for a comparison of community patterns and responses across regions with different species pools²². For these purposes, it is important that trait data are available in appropriate quality and quantity, and have broad taxon and regional coverage. Overcoming these barriers will foster collaboration among arachnologists and other researchers that aim for multi-taxa analyses^{15,23,24}.

Trait databases already exist for a number of taxonomic groups, such as plants²⁵, fish²⁶, amphibians²⁷, corals²⁸, reptiles²⁹, copepods³⁰, butterflies³¹, and ground beetles³², with a similar aim to accumulate and organize available data in a single repository. The success of such databases can be seen in the frequent use by many scholars³³. A general database of spider traits has not yet been developed. However, a range of spider traits can currently be found in several online resources, for example, body size of European species³⁴, cytogenetic

data³⁵, protein toxins of spiders³⁶, habitat and phenology of British (<http://srs.britishspiders.org.uk/>) and Czech spiders (<http://arachnobaze.cz/>), and various traits of ground-dwelling spiders (<https://portail.betsi.cnrs.fr>).

Recently, Lowe et al.¹⁰ initiated the establishment of a centralized database that aims to cover all spider traits and store data in a single place under FAIR (findable, accessible, interoperable, reusable) principles³⁷. Lowe et al.¹⁰ built the foundation of such database by detailed coverage of the trait definition, their standardization, input data types, database governance, geographic cover, accessibility, quality control, and sustainability. Furthermore, Lowe et al.¹⁰ recognized that the unification of the trait records can only be accomplished by careful examination of the data during the validation procedure.

Following the initiative¹⁰ here we present a curated global database which follows the FAIR principles and hosts a variety of traits recorded for spiders (**Fig. 1**). With the potential to grow indefinitely, so far we have already collected data for more than 7,000 spider taxa. The database has two main goals: 1) to collect and curate trait data on spiders from different sources, either (un)published or to be published in the future; and 2) to provide public access to these data under a CC BY licence facilitating their widespread use by researchers.

Methods

Definitions

We adopted a broad definition of traits for inclusion to our database: any measurable phenotypic (i.e., morphological, ecological, physiological, behavioural, etc.) characteristic of an individual or taxon. This may also include ‘pure’ traits³⁸ as well as the response to environmental conditions or a treatment^{39,40}. Traits can be either quantitative (continuous, integers, proportions) or categorical (qualitative, binary, and ordinal). Trait values can represent individual-level measurements (single observation) to higher taxonomic (species-, genus-, family-) level measurements (aggregates), often recorded as a statistic (mean, median, minimum, maximum). We do not consider descriptive molecular data (such as DNA or protein sequences) or faunistic records to be traits unless these contain reference to some trait (e.g., habitat type), as these have already established repositories such as GenBank® or the Global Biodiversity Information Facility (GBIF).

The definition of specific traits (including units for numerical traits or eligible values for categorical traits) was adopted from widely used definitions in a variety of published papers on spiders. To achieve semantic interoperability each trait is described by standardized terms (Table S1). Two types of ontologies, describing the process of data collection and traits themselves, were implemented during development of the database structure as suggested by Kissling et al.¹². The process of measurement, i.e. details of data collection is provided as metadata and the trait measured is given in the main table (see below).

To increase the interoperability of this database with other databases, the next step in the update of the database will be setting up an expert team to develop ontologies, detailed

vocabularies, and hierarchical structure for all traits. Some traits thus might be re-defined. This will not affect the current content but will prepare space for a harmonised collection of future data.

Database structure

We developed an online application and architecture called World Spider Trait database, currently in version 1.0 (<https://spidertraits.sci.muni.cz/>), to store and retrieve trait data on spider species (**Fig. 2**). The database is able to accommodate traits measured at any taxonomic level. As many trait values show variation (phenotypic plasticity) as a response to varying conditions, each trait record can be accompanied by extensive metadata, describing the conditions under which it was measured (such as treatment, sampling method, geographic location, habitat, date). The database was built to meet the FAIR principles: it is available at a public domain under open-access licence in a machine-readable format. This is enhanced by comprehensive online search options, and export capabilities.

The database has multi-layered structure. It is composed of a main table (**Fig. 1**) including five mandatory variables, namely (1) Original species name (taxon name as reported in the original source), (2) Trait abbreviation (unique abbreviation of each trait), (3) Trait value (measured value of a trait), (4) Method abbreviation (unique abbreviation of each method used to measure a trait), and (5) Reference abbreviation (unique abbreviation of each source). Several other variables are optional, namely Measure (type of the measured value), Sex, Life stage (ontogenetic stage), Frequency (relative frequency of occurrence), Sample size (total number of observations per record), Treatment (treatment conditions), Location abbreviation (unique identifier of a location), Latitude, Longitude, Altitude, Locality (the name or description of the place), Country, Habitat (habitat type according to a local classification), Microhabitat, Date, Note (any note related to a record), Row link (unique identifier of related measurements), and Reference (full reference). For a detailed description of each variable and examples see **Table 1**.

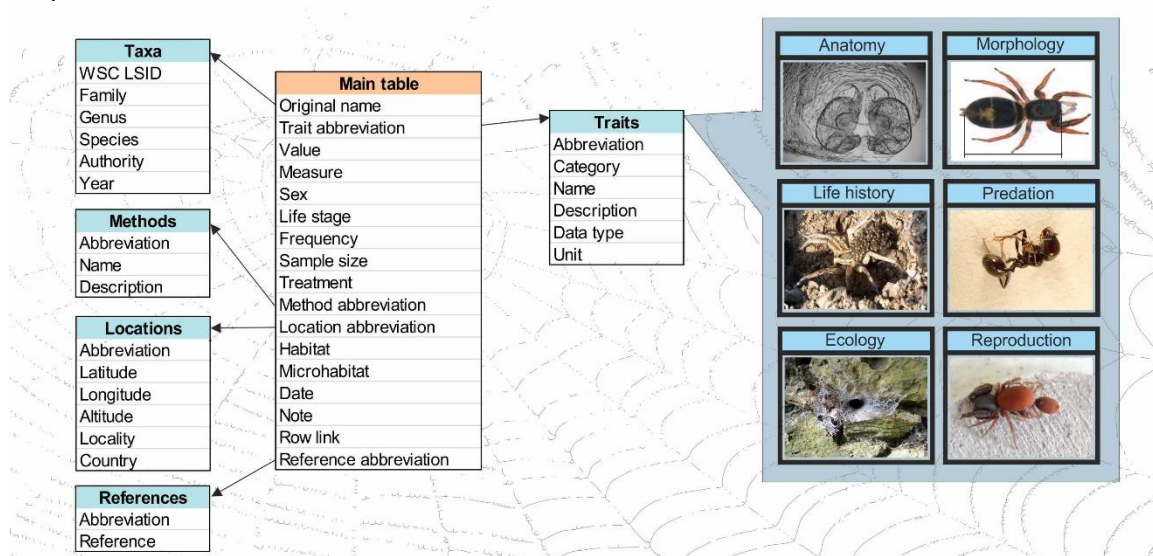


Fig. 1: A scheme of the database structure. There is the main table connected to five metadata tables. Examples of trait categories are given on the right. Photos: S. Pekár.

In the backend of the application, there are five additional metadata tables (extensions) which provide auxiliary information: (1) Taxa, (2) Locations, (3) Traits, (4) Methods, and (5) References. The Taxa table includes valid species or subspecies name, genus, family, LSID (Taxonomic identifier automatically retrieved from the World Spider Catalog¹), taxonomic authority and year. The content of this table is automatically updated on a weekly basis from the spider nomenclature information available in the World Spider Catalog¹, which contains valid Latin names and synonyms. Morpho-species do not have valid species names thus higher level categories (e.g. genus) are used optionally accompanied by additional information provided by the uploader in the Note variable. The Locations table includes country code, country name, locality name, coordinates, and its abbreviation. The Traits table contains Trait name, Category, Description, Data type, Unit, and its abbreviation. The Methods table includes method name, description and its abbreviation. References table includes full reference and its abbreviation. For more details see **Table 1**.

We defined 175 traits which are currently grouped into 13 categories according to the discipline (Anatomy; Biomechanics; Communication; Cytology; Defence; Ecology; Life-History; Morphology; Morphometry; Physiology; Predation; Reproduction) (**Table S1**). Information on the way a trait was measured is described in the Methods table. The provision of this metadata is mandatory during upload to ensure comparability of data. The Methods list includes field collection as well as laboratory methodology. Currently, there are 37 methods defined (**Table S2**). The included pre-defined traits, categories, and methods are meant to cover the majority of traits and methodologies in spider research; however, the architecture of the database is flexible enough that further traits, categories and methods can be added in the future, to accommodate new trait types and novel methodologies.

This database is hosted, developed, and maintained at the Department of Botany and Zoology of Masaryk University in collaboration with the University IT centre. It is connected to the World Spider Catalog¹, administered and curated by the core team members (**Fig. 2**).

Data upload procedure

Upon collection the data must be harmonised. Before a dataset can be submitted to the database, the data must be in a valid format (for a detailed description see <https://github.com/ookook/spider-trait-database/blob/master/docs/template.md>). For this purpose, we developed a MS Excel spreadsheet (Template) that should fit the great majority of trait types with predefined columns. The spreadsheet was designed to enable easy data manipulation by classical statistical software, such as R⁴¹. The template can be downloaded from the World Spider Trait database webpage (<https://spidertraits.sci.muni.cz/contribute>). It contains 31 columns, some of which are mandatory so they must be filled with appropriate numerical or character values. Eligible values for all columns can be found in the header of each variable, in the List of Traits (Table S1), and List of Methods (Table S2). If the input trait or method is not already defined the contributor should provide all of the following information to create a new trait or method: Trait category, trait name, trait description, trait data type, and trait unit in the case for missing

traits or method name and method description in the case of missing methods. Similarly, for references, the contributor either provides an abbreviation of a reference if it is in List of References or a full reference. Unpublished data are referenced as personal observations.

The data in the template then needs to be saved either as an .xls(x) or a comma-delimited.csv file and the file should be encoded as UTF-8 to assure compatibility with special (regional) characters. Once the template is uploaded the contributor must approve it using the tools within the web application.

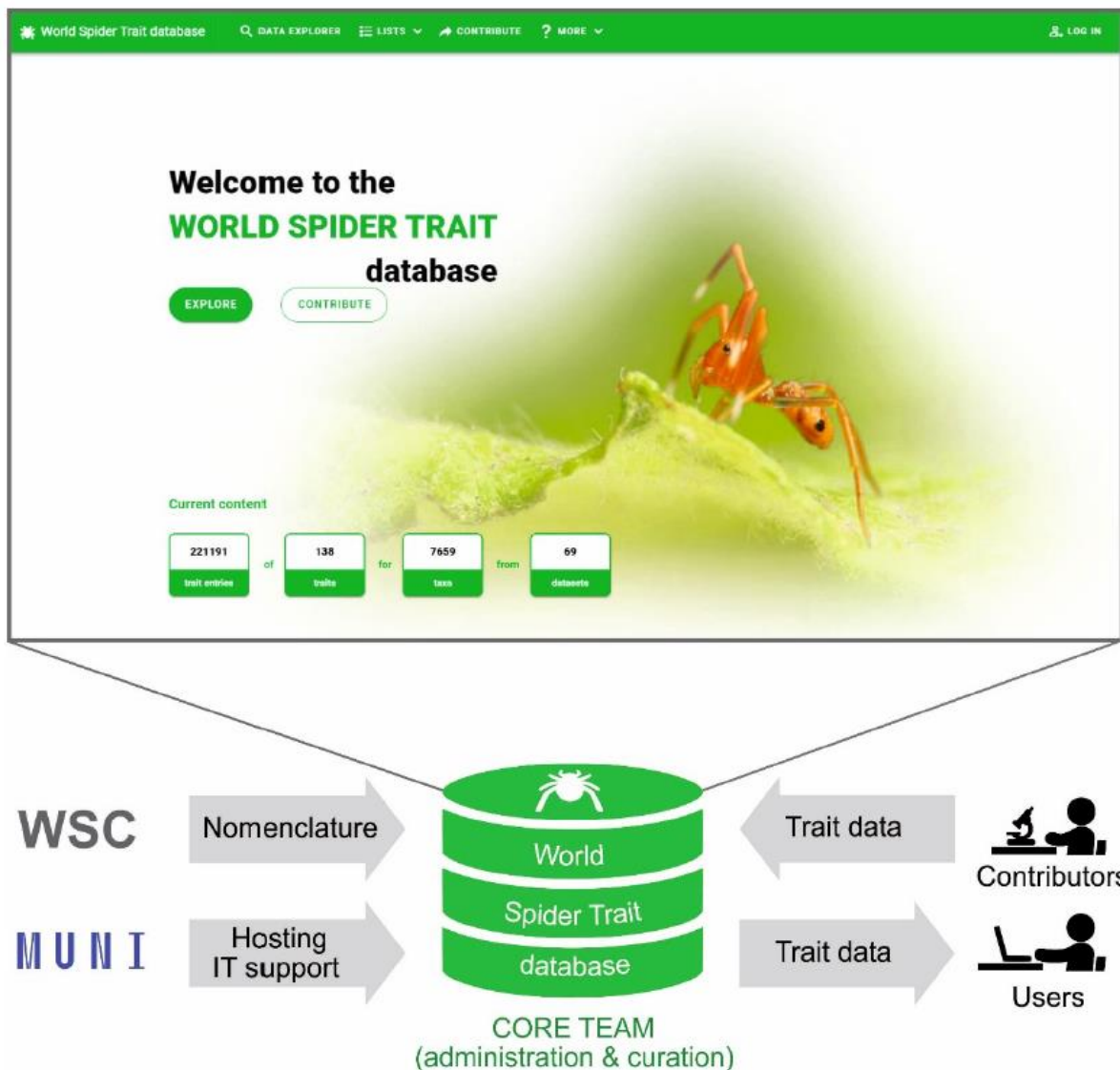


Fig. 2: The scheme of the World Spider Trait database application, depicting the role of contributing bodies and the frontpage of the webpage (<https://spidertraits.sci.muni.cz/>, accessed on March 5th, 2021). WSC stands for World Spider Catalog, MUNI stands for Masaryk University

Data Records

Integration of data from different sources was based on standardization and harmonisation. This involved conversion of trait values to comparable units/trait, use of controlled vocabulary in definition of traits, standardisation of eligible character values, and use of single spreadsheet format. Each record was accompanied by licence information and original source.

Currently, both published (from more than 1,000 publications) and unpublished data from diverse study designs (both descriptive and experimental) are included in the database with the citation of the original source⁴⁶. So far 70 datasets have been contributed with the total number of more than 221,000 records belonging to more than 7,500 taxa. Of these, 40 datasets (34.1% of records) are unlocked (i.e., freely accessible without registration). The remainder (i.e., embargoed datasets) are previously unpublished data compilations and can be viewed and downloaded by registered users only to ensure applicable authorship credits (see 'Usage Notes'). Registration and data usage is free under a CC BY licence. Embargoed data compilations may eventually become unlocked (e.g., once these have been used in published studies).

Geographical coverage of the database is global, but currently there are more records from Europe and South America than from other continents (**Fig. 3**)—a typical bias in biodiversity research⁴². Data on taxa from North America, Africa, and Asia are represented by very few records. The great majority of records available now come from Europe. Specifically, 20 datasets (66.1% of records) concern European species. This includes data on body size (2024 species), light & moisture preferences (1949 species), guild classification (1017 species), and conservation status (1557 species). In terms of traits, anatomical, behavioural, and physiological data are largely missing.

As for the taxonomic coverage, of 128 known spider families only two (Euctenizidae and Penestomidae) have no records in the database so far (**Fig. 4**). Several families (e.g., Gnaphosidae, Lycosidae, Salticidae, Sicariidae, Theridiidae) each have data for more than 40% of the 138 traits. But 38 families still have fewer than 5% of all traits covered. As for the number of records per family, most records come from the most speciose families, namely Linyphiidae, followed by Lycosidae, Theridiidae, and Salticidae (**Fig. 5A**). Because not every trait has been measured for every taxon, the taxon x trait matrix is highly incomplete (2.82% completeness, **Fig. 5B**). This is to be expected for a highly diverse and severely understudied taxonomic order. With respect to sex/stage, there are 33.6% records for adult males, 55.8% adult females, and 8.6 % for juveniles.



Fig. 3: Geographic coverage of the data in the database. Orange points represent geo-referenced records, while blue points are country centroids. There are records from 70 countries and 479 locations. The map was created using Google Maps.

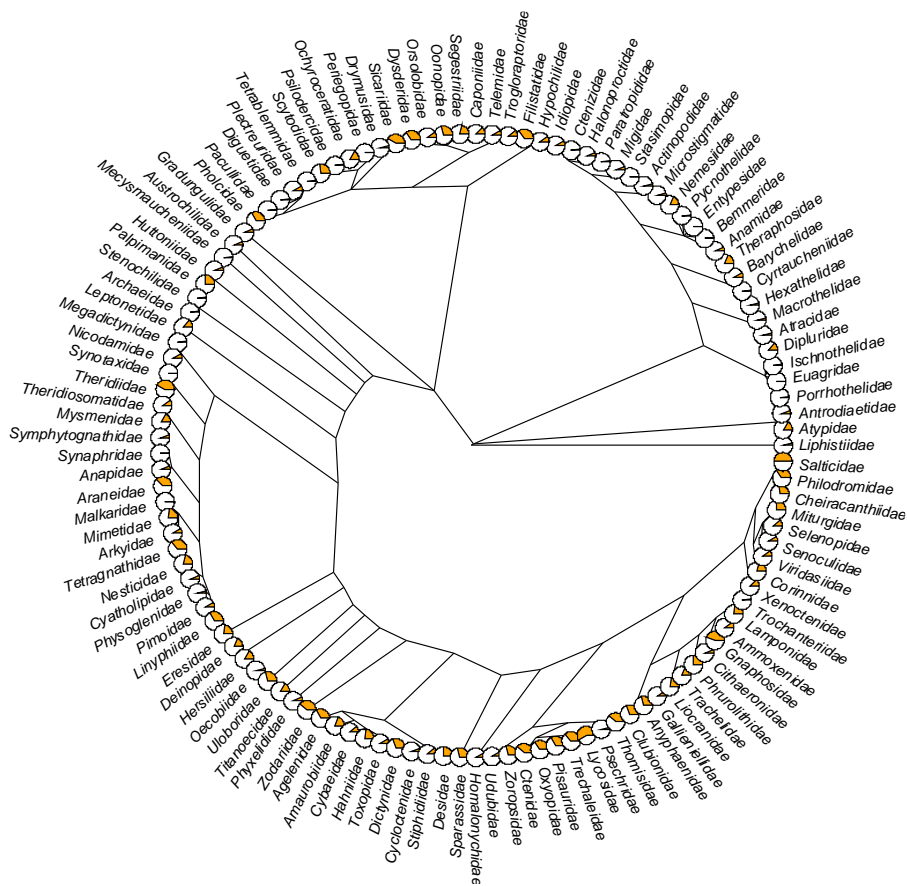


Fig. 4: Trait coverage mapped on the tree. The tree is on the family level (composed of 121 families which are represented in the database) with the proportion of the total number of traits (orange) displayed as pie charts (the fuller the pie the more traits). The tree was constructed based on the most recent phylogeny of spiders (Wheeler et al. 2017).

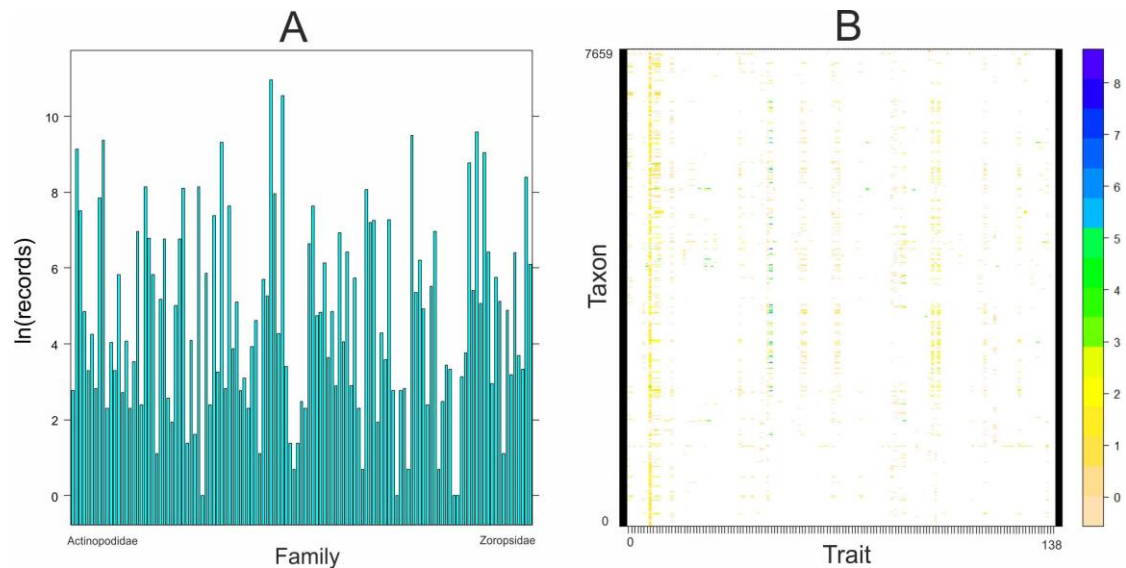


Fig. 5: Quantitative content of the database. A. Number of records (logarithmically transformed) for each family included in the database arranged alphabetically. B. The taxon by trait matrix representing the completeness. The most complete traits include body length (64% of taxa), followed by cephalothorax length (23%), and cephalothorax width (19%). Dots represent logarithmically transformed number of records per taxon. Taxon includes one of the following: subspecies, species, genus, or family.

The content of the database reflects real historic differences among geographic areas and disciplines. The database thus can be used to identify gaps and help to prioritise future areas for investigation to achieve more complete sets of records. To fill these gaps we plan to encourage contributions from specific areas, traits, and trait categories in the future. This can include collection of data from other repositories, extraction of data from publications, and archiving currently produced data. We will also ask curators of specialised spider trait databases to provide their data to be centrally stored here. Since many funders and journals now require data to be made publicly available, the database can be used as a permanent data archive option (an alternative to, e.g., Dryad or Figshare) provided that each contributed dataset meets standards of the database format which allows efficient reuse and synthesis. Each dataset obtains a unique URL and, in near future, it will be associated with a DOI provided by DataCite. In the future we expect to gather mainly data on new traits and new taxa and would like to encourage colleagues to contribute their datasets of both published and unpublished data. A coordinated effort is needed to achieve this goal.

To promote the process of data collection, we invite arachnologists to download the template and use it for data storage on their personal computers. At the same time, we ask arachnologists to get use to the vocabulary of the database, adopt definition of the traits that is used here (or suggest a different one) and develop protocols that follow the same standards. This will markedly enhance integration of their datasets with the database.

Technical Validation

Validation is performed at several steps during submission in order to retain only high quality records.

Firstly, a contributor is advised to search through the current database content in order to ensure that such (exact) data are not already included. It is also useful at this point to check whether the proposed trait(s) and method(s) are already defined. Contributors become eligible to upload their dataset after requesting registration from the administrator.

To upload a new dataset a contributor must specify the name of the dataset, their full name and email address. In addition, a contributor can specify authors of the dataset, author emails, mark whether the data can be immediately accessed or are under an embargo, and add any note. Then, the dataset sheet is created and the contributor is able to upload the data. The data is then imported to the temporary cache. During the upload process the web application checks the presence of eligible values in the following variables (Original name, Trait abbreviation, Value, Measure, Sex, Life stage, Frequency, Sample size, Method abbreviation, Latitude, Longitude, Altitude, Country, Date, Reference) and identifies duplicate records. Invalid records are highlighted to facilitate corrections. The taxonomy check includes existence of the name and match with a current valid name according to the World Spider Catalog¹.

At this stage, the contributor can view the dataset and must edit invalid cells in order to comply with the database requirements. Editing is done using the web application tools. When the contributor completes all changes and the dataset is valid, it can be sent to the administrator or editor for a review. The contributor can include a message to the editor when submitting the dataset for review in which the contributor can explain any problems the contributor had encountered while editing the dataset.

The administrator or editor is informed of a new dataset submission by an email. The dataset enters a second validation phase which can only be done by the administrator or editor. The administrator or editor must add new trait(s) and method(s) to the database, check for additional errors, such as extreme (unlikely) values of traits (e.g., resulting from typos, wrong digit separator, etc.), imprecise definition of new traits and methods, or an incorrect format of references. Once the dataset is validated by the administrator or editor it is published in the database. This means that all the data are transferred from the temporary import cache to the main database and becomes available to the general public. If the administrator or editor observes any problems, the dataset is rejected and sent back to the contributor with an email containing a description of the problem(s) to be fixed. Any dataset can be *post-hoc* corrected/alterred by the administrator or editor with/without contributors' consent.

Usage Notes

A user can view the whole content of the database using the Data Explorer within the online application. In the Data Explorer the user can apply filters (Family, Genus, Species, Original name, Trait category, Trait, Method, Location, Country, Dataset, References, Row links) to display selected content. The result can be displayed in a spreadsheet or in bar figure window. Selected data can then be downloaded in a .csv or .xlsx format. If the selected data contain data from datasets under embargo the user is given a warning. In order to download embargoed data the user has to send a request to the administrator or editor, who will then contact the dataset authors. All data with or without embargo can be download only after receiving login data.

In addition, the database provides an Application Programming Interface (API) to allow access to data via web platforms or software. An R package, named `spidR`⁴³, with few easy-to-use functions that allow downloading and pre-processing data from the database is now available. Resulting data frames can then be analysed with a variety of tools available in R⁴¹. Access of the embargoed data via API requires login as well.

As the trait value data can be a mixture of various statistics, it is important that the user checks the 'Measure' variable of each record and adopts appropriate procedures prior to analysis. Furthermore, due to inherent variation in most trait values, the user must consider conditions (such as habitat, altitude, treatment, etc.) under which it was measured. Not all conditions (e.g. hunger state, mating status, etc.) are recorded in the auxiliary variables, thus the user is strongly advised to study the original publication.

A number of traits included in this database are candidates of Essential Biodiversity Variables proposed by the Group on Earth Observations Biodiversity Observation Network^{12,13}. The traits are recorded with many metadata and thus allow quantification of intra-specific variation with respect to environmental conditions, space and time. These traits can be of societal relevance as they can be used in study spread of invasive species or biodiversity change.

Although the use of data is free, users are strongly encouraged to contribute their data particularly if they have not contributed yet following the simple 'first give, then take' principle. Only by these means the database will grow in quantity and frequency of use.

Contained data are publicly available under a Creative Commons Attribution license (CC BY 4.0), so that anyone can use received data under the condition of appropriate citation of this publication. In the case of datasets that have not been published and are under embargo, the user must agree with the dataset contributor on the conditions of use. Typically, this should include citation (URL or DOI) of the specific dataset in addition to the database citation.

Code Availability

The code of the web application is stored at GitHub (<https://github.com/ookook/spider-trait-database>) and is available under the GNU GPL v3.0. The phylogenetic tree was produced using functions within ape package⁴⁴ within R⁴¹.

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Supplementary information

Table S1: List of Traits, arranged alphabetically within trait categories.

Abbr.	Category / Name	Description	Data type	Unit	Eligible values
	<u>Anatomy</u>				
brsi	Brain size	Volume of CNS	real number	mm ³	
cuth	Cuticle thickness	Thickness of a cuticle on a body part	real number	mm	
nugl	Number of silk glands	Number of any silk glands per spinneret	integer		
prsy	Posterior respiratory system	type of posterior respiratory system (e.g. booklungs, tubular tracheae, lamella, absent)	character		
scle	Sclerotisation	Enhanced sclerotization of prosoma	character		
sigl	Silk gland size	Volume of any of the silk glands	real number	mm ³	
stfo	Sperm transfer form	State in which sperm is transferred to the female	character		
vgsi	Venom gland size	Volume of a venom gland	real number	mm ³	
	<u>Biomechanics</u>				
adhe	Web adhesion	Adhesion of capture thread	real number	MPa	
cspd	Climbing speed	Climbing speed (moving on a slope)	real number	cm/s	
rspd	Running speed	Running speed (moving horizontally)	real number	cm/s	
stra	Silk strain	Engineering strain of silk	real number	mm/mm	
stre	Silk strength	Engineering strength of silk	real number	Mpa	
toug	Silk toughness	Toughness of silk	real number	MPa	
	<u>Colouration</u>				
coop	Colouration of opisthosoma	Reflectance of dorsal side of opisthosoma at a certain wavelength (specify in Treatment variable)	real number	%	
copr	Colouration of prosoma	Reflectance of dorsal side of prosoma at a certain wavelength (specify in Treatment variable)	real number	%	
	<u>Cytology</u>				
chrn	Chromosome number	Diploid number of chromosomes	integer		

chrs	Sex chromosome system	The sex-chromosome system (e.g., XX0)	character		
chrt	Chromosome morphology	Type of chromosomes according to the position of the centromere (e.g., holocentric).	character		
	<u>Defense</u>				
modl	Model	Model imitated by species using camouflage and mimicry	character		Ant; beetle; wasp; snail; twig; branch; flower; etc.
prde	Primary defense	A strategy used prior to being detected by a predator	character		Cryptic (background matching); Cryptic (disruptive coloration); Cryptic (countershading); Aposematic; Batesian mimicry; Camouflage; Mullerian mimicry
pred	Predator	Taxonomical classification of a predator (e.g., wasp, bird, spider, etc.)	character		
retr	Retreat	Type of a retreat used to avoid predation	character		On web; in grass; under bark; silk sac; burrow; other
sede	Secondary defense	A strategy used after being detected by a predator	character		Death feigning; rapid escape; threatening posture; dazzle camouflage; startle; chemical deterrents; colour change; sound production
	<u>Ecology</u>				
balo	Ballooning	Occurrence of dispersal by ballooning (e.g., present)	character		
circ	Circadian activity	Hours of a day when the species is active (foraging, mating, web-building)	character		Diurnal; nocturnal; 1-24
disp	Dispersal time	Months at which dispersal occurs	character		January; February; March; April; May; June; July; August; September; October; November; December

girl	Global IUCN Red List category	Category of risk according to the global IUCN Red List guidelines	character		
					Forest; Savanna; Shrubland; Grassland; Wetlands; Rocky areas; Caves and Subterranean Habitats; Desert; Freshwater; Coastal; Urban, Agricultural; Other
habi	IUCN habitat	Habitat type according to the global IUCN classification	character		
halo	Habitat local CZ	Habitat type according to Czech habitat classification according to Chytrý M, Kučera T, Kočí M, Grulich V & Lustyk P. 2010. Habitat Catalogue of the Czech Republic. 2nd ed. Praha: Agentura ochrany přírody a krajiny ČR.	character		
lepr	Legal protection	Legal protection in national or subnational legislations	character		
ligh	Light	Light gradient according to Entling W, Schmidt MH, Bacher S, Brandl R & Nentwig W. 2007. Niche properties of Central European spiders: Shading, moisture and the evolution of the habitat niche. <i>Global Ecology and Biogeography</i> 16(4): 440–448.	real number		
lig2	Light 2	Light gradient according to Buchar J & Růžička V. 2002. Catalogue of spiders of the Czech Republic. Praha, Peres.	character		
mdl	Regional non-IUCN Red List category	Category of risk according to the regional guidelines (non-IUCN)	character		
miha	Microhabitat	Habitat where species occurs	character		among stones, bare ground, herbs, bushes, foliage, litter, etc.
moi1	Moisture 1	Moisture gradient according to Entling W, Schmidt MH, Bacher S, Brandl R & Nentwig W. 2007. Niche properties of Central European spiders: Shading, moisture and the evolution of the habitat niche. <i>Global Ecology and Biogeography</i> 16(4): 440–448.	real number		
moi2	Moisture 2	Moisture gradient according to Buchar J & Růžička V. 2002. Catalogue of spiders of the Czech Republic. Praha, Peres.	character		Dry, semi-humid. If possible give frequency (in field 'frequency'): 1 (preferred value), 0.5

					(primary value), 0.1 (marginal value)
ovws	Overwintering stage	Occurrence of overwintering (e.g., present)	character		
phen	Phenology	Months at which adult stage occurs	character		January; February; March; April; May; June; July; August; September; October; November; December
rasi	Range size	Area of the species distribution range	real number	km ²	
regl	Regional IUCN Red List category	Category of risk according to the regional IUCN guidelines	character		
soci	Social degree	Degree of sociality	character		Solitary, subsocial, colonial, quasisocial, social
strt	Stratum	Horizontal stratum occupied	character		Underground; ground; herb layer; shrub layer; tree trunks; canopy; wall
suaf	Subterranean affinity	Degree of subterranean affinity	character		Troglobiont, troglophile
	<u>Life History</u>				
indu	instar duration	Number of days spent in a certain ontogenetic stage (egg, larva, or instar) at a certain temperature (specified in Treatment variable)	integer	days	
inst	Number of instars	Total number of instars, beginning with the first free instar and ending with the adult stage	integer		
lonv	Longevity	Number of days from hatching to death	integer	days	
mort	Mortality	Mortality either natural or due to any treatment	real number	%	
sexr	Sex ratio	Number of males divided by the number of females	real number		
surv	Survival	Proportion of surviving individuals	real number	%	
	<u>Morphology</u>				
alsl	Spinneret ALS	Total length of anterior lateral spinneret (from base to tip)	real number	mm	
crib	Cribellum	Presence of functional cribellum and calamistrum (e.g., present)	character		
ente	Entelegyne	Presence of epigyne in females (e.g., present)			

eyes	Eye number	Total number of eyes	integer		
flat	Body flattening	Significantly flattened body as an adaptation to shelter in crevices	character		
nusp	Spine number	Number of erectable spines (macrosetae) on the prolateral side of leg I (that play a role in the formation of the capture basket)	integer		
scoa	Scopula area	Area of scopula hairs on leg segments	real number	mm ²	
scod	Scopula density	Number of scopula hairs per area on a leg segment	real number	mm ²	
spin	Spinnerets	Total number of functional spinnerets	integer		
	<u>Morphometry</u>				
abhe	Abdomen height	Opisthosoma height at highest point	real number	mm	
able	Abdomen length	Opisthosoma length from anterior to posterior along longitudinal axis (excl. petiole and spinnerets)	real number	mm	
abwi	Abdomen width	Opisthosoma width at widest point	real number	mm	
aled	ALE	Diameter of one anterior lateral eye	real number	mm	
alsl	Spinneret ALS	Total length of anterior lateral spinneret (from base to tip)	real number	mm	
amed	AME	Diameter of one anterior median eye	real number	mm	
bodm	Body mass	Body mass (in a normal nutritional condition)	real number	g	
bole	Body length	Total body length (from carapace frontal, excl. chelicerae, to opisthosoma posterior, excl. spinnerets)	real number	mm	
cehe	Cephalothorax height	Height of prosoma at the highest point (from sternum most ventral to carapace most dorsal)	real number	mm	
cele	Cephalothorax length	Length of prosoma (carapace) along the longitudinal body axis	real number	mm	
cewe	Cephalothorax width	Width of prosoma (carapace) at the widest point	real number	mm	
chle	Chelicerae basal part (paturon) length	Length of cheliceral base segment (paturon) along external margin	real number	mm	
cox1	Coxa I length	Coxa length of leg I	real number	mm	
cox2	Coxa II length	Coxa length of leg II	real number	mm	
cox3	Coxa III length	Coxa length of leg III	real number	mm	
cox4	Coxa IV length	Coxa length of leg IV	real number	mm	
criw	Cribellum width	Width of cribellum or colulus	real number	mm	

ctar	Claw tuft area	Projected area of adhesive foot pad (claw tuft) on leg IV	real number	mm ²	
ctde	Claw tuft density	Density of adhesive foot pad (claw tuft) on leg IV, i.e. number of tenent setae per area unit	integer		
eggs	Egg size	Diameter of an egg	real number	mm	
eggv	Egg volume	Volume of an egg	real number	mm ³	
epaw	Epigyne anterior plate width	Width of anterior border of epigyne plate	real number	mm	
epcw	Epigyne central plate width	Width of central border of epigyne plate	real number	mm	
eple	Epigyne length	Length of epigynal plate	real number	mm	
eppw	Epigyne posterior plate width	Width of posterior border of epigyne plate	real number	mm	
eyew	Eye region width	maximum width of eye region	real number	mm	
fale	Fang length	Cheliceral fang length from base articulation to the tip (measured along the median arc)	real number	mm	
fem1	Femur I length	Femur length of leg I (measured between condyles)	real number	mm	
fem2	Femur II length	Femur length of leg II (measured between condyles)	real number	mm	
fem3	Femur III length	Femur length of leg III (measured between condyles)	real number	mm	
fem4	Femur IV length	Femur length of leg IV (measured between condyles)	real number	mm	
l1le	Leg I length	Total length of one leg from the first (front) leg pair, excluding coxa and trochanter	real number	mm	
l2le	Leg II length	Total length of one leg from the second leg pair, excluding coxa and trochanter	real number	mm	
l3le	Leg III length	Total length of one leg from the third leg pair, excluding coxa and trochanter	real number	mm	
l4le	Leg IV length	Total length of one leg from the fourth leg pair, excluding coxa and trochanter	real number	mm	
met1	Metatarsus I length	Metatarsus length of leg I (measured between condyles)	real number	mm	
met2	Metatarsus II length	Metatarsus length of leg II (measured between condyles)	real number	mm	
met3	Metatarsus III length	Metatarsus length of leg III (measured between condyles)	real number	mm	
met4	Metatarsus IV length	Metatarsus length of leg IV (measured between condyles)	real number	mm	

ocdi	Ocular distance	Sum of diameters of one side of the caparace eyes (1 ALE, 1 PLE, 1 PME, 1 AME)	real number	mm	
pat1	Patella I length	Patella length of leg I (measured between condyles)	real number	mm	
pat2	Patella II length	Patella length of leg II (measured between condyles)	real number	mm	
pat3	Patella III length	Patella length of leg III (measured between condyles)	real number	mm	
pat4	Patella IV length	Patella length of leg IV (measured between condyles)	real number	mm	
pled	PLE	Diameter of one posterior median eye	real number	mm	
plsl	Spinneret PLS	Total length of posterior lateral spinneret (from base to tip)	real number	mm	
pmed	PME	Diameter of one posterior lateral eye	real number	mm	
pmsl	Spinneret PMS	Total length of posterior median spinneret (from base to tip)	real number	mm	
ptal	Palpal tarsus length	Length of palpal tarsus in males	real number	mm	
ptwi	Palpal tarsus width	Width of male palpal tarsus	real number	mm	
scoc	Scopula cover	Relative area of the prolateral side of leg I segment(s) covered with hairy adhesive pad (scopula, excluding claw tufts)	real number	mm ²	
stle	Sternum length	Width of sternum at widest point	real number	mm	
stwi	Sternum width	Length of sternum along the longitudinal axis	real number	mm	
tale	Tegular apophysis length	Length of tegular apophysis on male bulbus	real number	mm	
tar1	Tarsus I length	Tarsus length of leg I (measured between condyles)	real number	mm	
tar2	Tarsus II length	Tarsus length of leg II (measured between condyles)	real number	mm	
tar3	Tarsus III length	Tarsus length of leg III (measured between condyles)	real number	mm	
tar4	Tarsus IV length	Tarsus length of leg IV (measured between condyles)	real number	mm	
tawi	Tegular apophysis width	Width of tegular apophysis on male bulbus	real number	mm	
tib1	Tibia I length	Tibia length of leg I (measured between condyles)	real number	mm	
tib2	Tibia II length	Tibia length of leg II (measured between condyles)	real number	mm	
tib3	Tibia III length	Tibia length of leg III (measured between condyles)	real number	mm	
tib4	Tibia IV length	Tibia length of leg IV (measured between condyles)	real number	mm	
tro1	Trochanter I length	Trochanter length of leg I (measured between condyles)	real number	mm	
tro2	Trochanter II length	Trochanter length of leg II (measured between condyles)	real number	mm	
tro3	Trochanter III length	Trochanter length of leg III (measured between condyles)	real number	mm	
tro4	Trochanter IV length	Trochanter length of leg IV (measured between condyles)	real number	mm	

	Physiology				
gluc	Glucose content	Amount of glucose in a wet mass	real number	µg/mg	
ld50	Venom toxicity	LD50 of venom on Drosophila prey	real number	nl venom/ mg fly	
pydr	Drought tolerance	Relative humidity the spider can tolerate	real number	%	
pytl	Lower thermal limit	Temperature limit at which growth occurs	real number	°C	
pymr	Resting metabolic rate	Oxygen consumption per time when inactive	real number	W	
pysb	Submerging time	Time of surviving under water	real number	h	
pytu	Upper thermal limit	Temperature limit at which growth occurs	real number	°C	
prot	Protein content	Amount of proteins in a wet mass	real number	µg/mg	
trig	Triglyceride content	Amount of triglycerides in a wet body mass	real number	µg/mg	
	Predation				
cons	Consumption time	Time spent consuming certain prey (specified in Treatment variable)	real number	h	
guil	Hunting guild	Ecological hunting guild according to Cardoso P, Pekár S, Jocqué R & Coddington JA 2011. Global patterns of guild composition and functional diversity of spiders. PLoS One 6(6): e21710.	character		Sensing web weavers; sheet web weavers; space web weavers; orb web weavers; specialists; ambush hunters; ground hunters; other hunters.
klep	Kleptoparasitism	Occurrence of kleptoparasitism (e.g., present)	character		
nich	Trophic niche breadth	Levin's standardised index of niche breadth according to Hurlbert SH 1978. The measurement of niche overlap and some relatives. Ecology 59(1): 67-77.	real number		
para	Paralysis latency	Time between attack and prey immobilisation	real number	min	
prdi	Prey diversity	Shannon-Weaver index of diversity of captured prey as a measure of niche breadth	real number		
prek	Overkilling	Proportion of prey items killed but not consumed	real number	%	
prec	Prey capture	Mode of prey capture	character		Bite-and-release; grab-and-hold; wrapping; throwing silk; other

prem	Satiation	Number of prey items killed and consumed per certain time interval (specified in Treatment variable)	integer		
preo	Prey order	Taxonomic order of an organism the spider preys on	character		
prey	Prey	Type of organism the spider preys on (e.g., egg, caterpillar, imago)	character		
prsi	Prey size	Prey size (total body length)	real number	mm	
stsp	Strike speed	Time to complete a predatory strike (start of strike to first bite)	real number		
weba	Web area	Size of web projected in a 2-dimensional space	real number	cm ²	
webb	Web building	Use of a web for prey capture (not a retreat) (e.g., present)	character		
webd	Web diameter	Linear dimension of a web	real number	cm	
webt	Web type	Type of capture web	character		Orb web; cob web with gumfoot lines; sheet web; canopy web; space web; open tube; tube with trap door; tube with signaling lines; single line; other
webv	Web volume	3-dimensional size of a web	real number	cm ³	
	<u>Reproduction</u>				
coco	Coersive copulation	Presence of coercive mating indicated by causing injuries to the other sex (present, absent)	character		
codi	Cocoon diameter	Maximum diameter of the cocoon	real number		
coty	Courtship type	Sensual modality used during courtship (verbal description)	character		
codu	Courtship duration	Time from starting the courtship to the beginning of copulation	real number	min	
duma	Duration of mating	Total mating time	real number	min	
eggm	Eggsac mass	Weight of an eggsac	real number	g	
eggn	Number of eggs/sac	Number of eggs in a clutch (eggsac) / eggsac order	integer		
egsn	Number of eggsacs	Total number of eggsacs produced by a female during her life	integer		
eplu	Epigyne plugging	Mode of blocking access to the female epigyne	character		Excretion; embolus; none; other
fert	Fertility	Number of hatched offspring	integer		

maca	Maternal care	Extent of maternal care	character		None; guarding egg sac; guarding egg sac and spiderlings
maph	Matriphagy	Presence of matriphagy (i.e., offspring consuming tissue of their mother) (e.g., present)	character		
mapo	Mating position	Type of a mating position (e.g., type 1, 2, 3) according to Foelix R F. 2011. Biology of Spiders. 3rd ed. New York: Oxford University Press.	character		
nuin	No. of insertions	Total number of insertions during copulation	integer		
nupa	No. of partners	Total number of mated partners	integer		
ovip	Oviposition	Time to oviposition (following the first mating)	real number	days	
sexc	Sexual cannibalism	Occurrence of sexual cannibalism and the sex of cannibal (e.g., present/female)	character		
	<u>Sound</u>				
fred	Dominant frequency	The peak frequency of the sound produced	real number	Hz	
freq	Lower frequency range	The minimum frequency of the sound produced	real number	Hz	
freu	Upper frequency range	The maximum frequency of the sound produced	real number	Hz	
soun	Sound production	Mechanism of sound production (e.g., stridulation)	character		
sour	Sound source	Organ used to produce sound (e.g. chelicera and pedipalp)	character		

Table S6: List of Methods. For each method there is an abbreviation, name and short description.

Abbreviation	Method name	Description
bea	Beating	Capture by beating over net
cit	Citizen Science	Observation collected through citizen science
col	Colorimetry	Concentration assessment of a chemical compound in a homogenate
dis	Dissection	
exp	Expert-Base	Assessed based on expert opinion
fie	Field Observation	Observation performed in nature
fot	Photoeclector trapping	Capture by photoeclector
fun	Functional Response	Experiment of functional response
gut	Gut-Content Analysis	Molecular analysis of gut content
han	Hand Collection	Capture by individual hand sampling
kar	Karyology	Karyology on dissected tissue
lab	Laboratory Observation	Observation performed under laboratory conditions
mal	Malaise Trapping	Capture by Malaise traps
mic	Microscopic Measurement	Measurement done under microscope or in micro-photographs
mor	Morphometry	Length determination based on microscopy
mov	Movement Measurement	Measurements done using video-tracking software (e.g., Ethovision)
mul	Multiple data analysis	Analysis of results of former multiple studies
na	Not available	This information is not available
olf	Oloactometry	Measurement done using olfactometer
pan	Yellow Pan Trapping	Capture by yellow pan traps
pho	Photographic Analysis	Analysis of photographs
pro	Protein content	Measurement of protein content using Bradford's method
ptf	Pitfall Trapping	Capture by pitfall traps
res	Respirometry	Measurement done using respirometer
she	Shelter Trapping	Capture by shelters (e.g. bark bands)
sie	Sieving	Capture by sieving
sou	Sound Recording	Sound recorded by a recorder
spe	Spectrophotometric Measurement	Measurement done using spectrophotometer
suc	Suction trapping	Capture by a suction trap placed in the air
swe	Sweeping	Capture by sweeping net

tem	Transmission electron microscopy	Transmission electron microscopy using standard protocol for chemically fixed samples
the	Thermometry	Measurement done using temperature controlled chamber
tox	Toxicology	Toxicology bioassays
vac	G-VAC sampling	Capture by sucking up device.
ven	Venom potency test	Test of venom potency using a standardized protocol (specified in trait or notes)
web	Web Analysis	Analysis of the web content
wei	Weighing	Weighing on a lab scale (i.e. analytical balance)

ANNEXE.3

Nouvelle espèce de *Hypaeus* Simon (Araneae : Salticidae : Salticinae : Amycini) basée sur la taxonomie intégrative

New species of *Hypaeus* Simon (Araneae: Salticidae: Salticinae: Amycini) based on integrative taxonomy

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Abstract

A new species of *Hypaeus* Simon is described from French Guiana based on both sexes, *Hypaeus olympeae* **sp. nov.** We employed morphological evidence, field observation, as well the mitochondrial COI rapidly evolving loci to confirm that both males and females belongs to the same species. Finally, nine species are newly added to the list of salticids from French Guiana and 12 COI sequences corresponding to four so far unsequenced *Hypaeus* species are added to GenBank.

Key-words: Jumping spiders, Barcoding, Cytochrome C Oxydase Subunit 1, Taxonomy, French Guiana

Introduction

Neotropical spider's taxonomy is scarce (Scharff *et al.* 2003), partly because spiders are really diverse in neotropical forests (Cardoso *et al.* 2011; Privet & Pétilon 2018) and the human and material costs needed for their study are high; but this scarcity is also due to the huge proportions of rare species and juveniles in tropical assemblages (Coddington *et al.* 2009) and the difficulty to describe species based on only one specimen and therefore on a single sex and on juveniles. Spiders are a model group for ecological studies (Birkhofer & Wolters 2012; Cardoso *et al.* 2011; Malumbres-Olarte *et al.* 2018; Moya-Laraño *et al.* 2013) and the only group to be exclusively predatory among the dominant terrestrial arthropods (Birkhofer & Wolters 2012; Pekár & Toft 2015). Improving their taxonomy is thus crucial to understand neotropical diversity and ecology.

Within the neotropical forests of the Amazon, the most abundant and speciose spiders are the jumping-spiders (Salticidae; Bodner & Maddison 2012) and the richest subfamily is Amycinae (Araújo & Ruiz 2015; Maddison 2015). Among them, *Hypaeus* Simon 1900 may be one of the richest genera with 28 described species distributed from south to central America (World Spider Catalog 2021).

Species of *Hypaeus* are morphologically recognizable from their high carapaces, plumose setae over front eyes, pluridentate chelicerae with 4-5 teeth on promargin and 3-6 on retromargin, mastidia on male chelicerae and third leg longer than fourth (Galiano, 1968; Ruiz & Madisson 2015). However, *Hypaeus* is still poorly sampled and described and the boundaries of the genus are not completely understood (Araújo & Ruiz 2015).

Galiano (1963, 1968) redescribed and revised 18 *Hypaeus* species described by Crane (1943), Mello-Leitão (1948), Peckham & Peckham (1885), Simon (1900) and Taczanowski (1871, 1878). She also transferred two species to this genus, *Amycus mystacalis* (Taczanowski, 1878) and *Triptolemus benignus* (Peckham & Peckham, 1885); and synonymized one, *Mago budoninus* (Caporiacco, 1954). Two others were described by Crane, *H. duodentatus* Crane, 1943, and by Caporiacco, *H. barromachadoi* Caporiacco, 1947. Recently, the male and the female of the type species of the genus *Hypaeus*, *H. taczanowskyii* (Mello-Leitao, 1948), were redescribed by Araújo & Ruiz (2015). The same authors added four new species to the genus, *H. tridactylus*, *H. famoratus*, *H. poseidon* and *H. terramediae* Araújo & Ruiz 2015, and transferred *Hasarius pauciaculeis* (Caporiacco, 1947) to *Hypaeus*. The last issue from Martinez & Galvis (2017) added three new species, *H. arhuaco*, *H. proszynskii* and *H. varzea* Martinez & Galvis, 2017. Of the resulting 28 *Hypaeus* species, 17 have been described only from males (Araújo & Ruiz 2015; Martinez & Galvis 2017; World Spider Catalog 2019).

Methods such as the combination of morphology with DNA barcoding should help to overtake the limitations of tropical spider's taxonomy linked to juveniles and rarity. Phylogenetic analyses are also needed to resolve the relationships within this genus (Ruiz *et al.* 2019). However, only sequences for two *Hypaeus* species, *H. mystacalis* (Taczanowski, 1878) and *H. miles* (Simon, 1900), are available to date.

One hundred and two species of Salticidae are currently listed for French Guiana (Courtial *et al.* 2014; Vedel *et al.* 2013) and among them three *Hypaeus* species: *H. flavipes* (Simon, 1900), *H. porcatus* (Taczanowski, 1871) and *H. taczanowskii* (Mello-Leitao, 1948). During our last expeditions conducted in French Guiana (see Privet *et al.* 2018; Privet & Petillon 2018), in the National Nature Reserves of La Trinité and Les Nouragues, we collected numerous species of Salticidae and among them several specimens of the genus *Hypaeus*; this includes a species new to science. In this study, we used a combination of morphology and DNA barcoding targeting COI to match and describe the male and female from a new species, *Hypaeus olympeae* **sp. nov.**, produce sequences for four other *Hypaeus* species never sequenced so far, and add nine species to the list of salticids from French Guiana.

Material and Method

Taxon sampling

Taxa included in this study are 12 individuals of salticids belonging to the genus *Hypaeus*. They were collected in La Trinité (4°35'20"N; 53°18'1"W) and Les Nouragues (4°04'18"N; 52°43'57"W) Nature Reserves (French Guiana) during two surveys conducted in 2010 and 2013 (see Privet *et al.* 2018; Privet & Petillon 2018). In these reserves, seasonally flooded (Aya and Pararé) and summit inselberg (La Roche Bénitier and Nouragues) forests were sampled. Inselbergs are rocky outcrops rising abruptly from the surrounding landscape where little research has been devoted to invertebrates, especially spiders (Privet *et al.* 2018). The 12 specimens were morphologically identified; 6 accessions were assigned to *H. taczanowskii* and 4 to *H. porcatus*. Two specimens, impossible to assign to any of the currently recognized *Hypaeus* species, correspond to the new species described here, *Hypaeus olympeae* **sp. nov.** Total DNA of the 12 *Hypaeus* specimens was then extracted using non-destructive method (see below).

Specimens

The type material examined is deposited at the Muséum national d'Histoire naturelle (MNHN, Paris). Preserved specimens were studied using an OlympusSZX9 stereomicroscope with a Moticom5 (5.0MP) camera. Living holotype male and paratype female were photographed with a Canon EOS 450 D digital reflex camera with a 60 mm macro lens. The epigyne was macerated in 10% KOH. The specimens were preserved in 70% ethanol. In order to make easier comparison between *Hypaeus* spp. recently described by Araújo & Ruiz (2015), measurements (in millimeters) were taken according to Edwards (2004). The following abbreviations are used:

AME = anterior median eyes

co = copulation opening

dg = digital gland

eb = embolus base

et = embolus tip

po = pocket

sp = spermathecae

ta = tibial apophysis

RNN = Réserve Naturelle Nationale (National Nature Reserve)

MNHN = Muséum national d'Histoire naturelle, Paris.

The drawings of male individuals of Galiano (1963, 1968), Crane (1943), Ruiz & Brescovit (2008), Araujo & Ruiz (2015) and Martinez & Galvis (2017), as well as the reviewing of type specimens stored at the MNHN (Paris, France), allowed us to identify the new species *Hypaeus olympeae* **sp. nov.** collected in French Guiana.

DNA extraction, amplification, sequencing and data assembly

DNA was extracted using DNeasy 96 Blood and Tissue Kit (Qiagen) following manufacturer's recommendations. The entire specimens were directly placed in lysis buffer with proteinase K overnight to extract DNA without compromising morphological requirements for further examination (Paquin & Vink 2009). The standard animal DNA barcode fragment of the mitochondrial cytochrome-c-oxidase subunit 1 (COI) was targeted by PCR using the primers C1-J-1718 "SPID" (Simon *et al.* 1994) and C1-N-2776 (Hedin & Maddison 2001). PCR reactions were performed in 25 μ L and contained 0.5X PCR Buffer, 0.2 mM dNTPs, 1 mM MgCl₂, 0.15 μ M of each primer, 0.02 U/ μ L of Taq polymerase (GoTaq, Promega) and 2 μ L of DNA. PCR amplification started with an initial 94°C denaturation step for 2 min, followed by 35 cycles of (i) denaturation at 94°C for 45 s, (ii) annealing at 50°C for 45 s, and (iii) extension at 72°C for 60 s; a final 72°C extension step lasted 10 min. Sequencing of PCR products was performed by Genoscreen (Lille, France) using the same primers than for amplification. Sequence fragments were imported, assembled and edited in Geneious 6.1.8 (Biomatters Ltd., Auckland, New Zealand). All sequences, with voucher information, are archived in GenBank (Table 1).

Phylogenetic analysis

The taxonomic sampling used for the phylogenetic analyses included the 12 sequences newly generated for the study as well as one GenBank accession of *Sarinda cutleri* (Richman, 1965) (JX145669), a closely related species (see Maddison *et al.* 2014) that served as outgroup. All sequences were aligned in Geneious using MAFFT v.7.017 (Katoh & Standley 2013).

The resulting COI matrix was subjected both to Bayesian inference (BI) and maximum likelihood (ML) analyses. We first searched for the best-fitting nucleotide substitution model using the Akaike information criterion (AIC) estimated by MrModeltest v.2.3 (Nylander 2004); the GTR + G model was selected and assigned to all following phylogenetic analyses. The software MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001) and RaxML-HPC v.8.1.24 (Stamatakis 2014) implemented on the CIPRES Science Gateway (Miller *et al.* 2010) platform were used to perform BI and ML analyses, respectively. MrBayes analyses constituted two independent parallel runs of four Markov chains each, implemented for one million generations and

sampled every 100 generations. Adequate mixing of the Markov chains and convergence of the two runs were confirmed with Tracer v1.6 (Rambaut *et al.* 2014). After removing a 10% burnin, the remaining trees were used to generate a 50% Bayesian majority-rule consensus tree. For the RaxML analyses, node support was assessed using a rapid bootstrapping algorithm with 1000 bootstrap iterations.

Table 1 : Summary of GenBank accession numbers, species name and voucher information (site coordinates are given in the Material and Methods) for the sequences newly generated for the study. [INFORMATION INTENDED FOR THE REVIEW PROCESS ONLY: The sequences generated for the present study are in the process of being submitted to GenBank. Once the GenBank accession numbers for all these sequences have been generated, we will update the table].

GenBank accessions	Name in topology	Voucher	Collection location	Sex
x	<i>Hypaeus olympeae</i> 1	ACAV07 3	La Trinité, French Guyana	♂
x	<i>Hypaeus olympeae</i> 2	ACAV07 2	La Trinité, French Guyana	♀
x	<i>Hypaeus porcatus</i> 1	NPTN11	Les Nourages, French Guyana	♀
x	<i>Hypaeus porcatus</i> 2	AQJ5	La Trinité, French Guyana	♀
x	<i>Hypaeus porcatus</i> 3	AQN1	La Trinité, French Guyana	♂
x	<i>Hypaeus porcatus</i> 4	AQJ5	La Trinité, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 1	NITJ3	Les Nouragues, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 2	NIQN9	Les Nouragues, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 3	IQN10	Les Nouragues, French Guyana	♂
x	<i>Hypaeus taczanowskii</i> 4	NPQJ7	Les Nouragues, French Guyana	♀
x	<i>Hypaeus taczanowskii</i> 5	PQJ4	Les Nouragues, French Guyana	♀
x	<i>Hypaeus taczanowskii</i> 6	NPQJ5	Les Nouragues, French Guyana	♀

Results

Class Arachnida Cuvier, 1812

Order Araneae Clerck, 1757

Family Salticidae Blackwall, 1841

Subfamily Salticinae Blackwall, 1841

Tribe Amycini F.O Pickard-Cambridge, 1900

Genus *Hypaeus* Simon, 1900

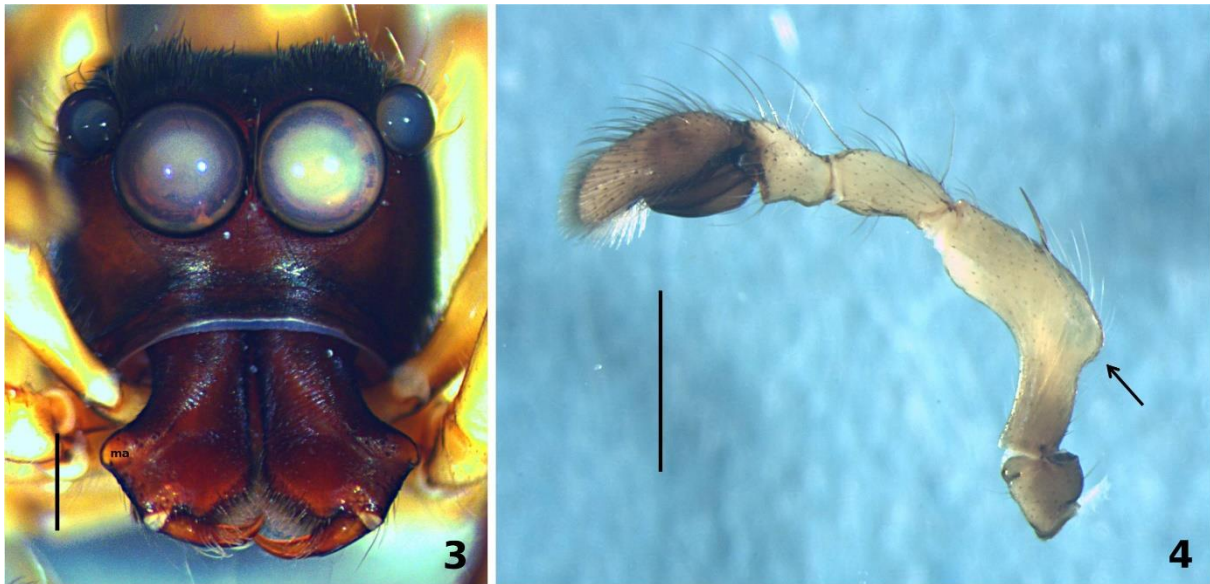
Hypaeus Simon, 1900: type species *Acragas taczanowskii* Mello-Leitão, 1948.

***Hypaeus olympeae* Courtial & Picard sp. nov.**



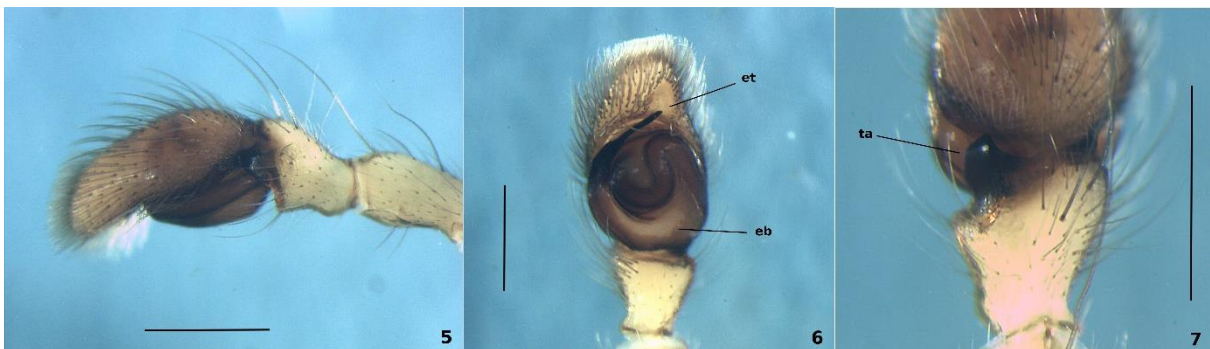
Figures 1 – 2

Hypaeus olympeae sp. nov. 1 male, dorsal view, scale 0,5mm; 2. Female, dorsale view, scale 1mm.



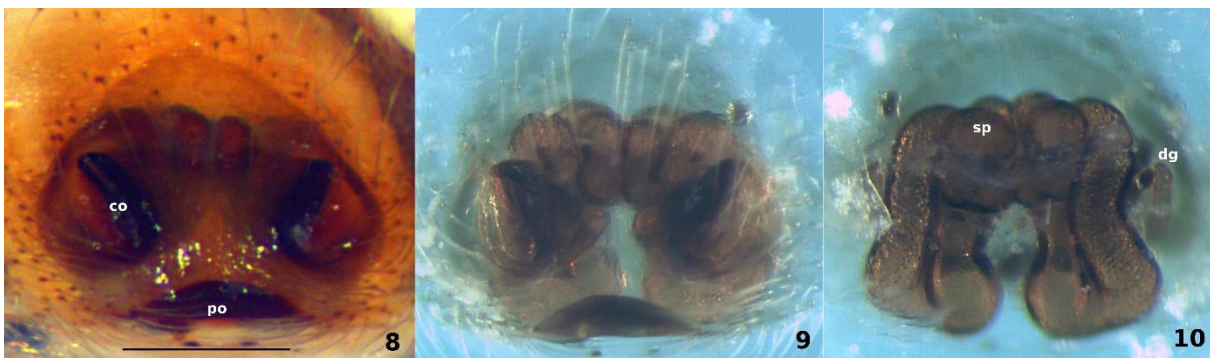
Figures 3 – 4

Hypaeus olypeae **sp. nov.** male. 3. Chelicerae detail (ma: mastidion), scale 0,5mm; 4. Left male palp with bump on femur (arrow), scale 1mm.



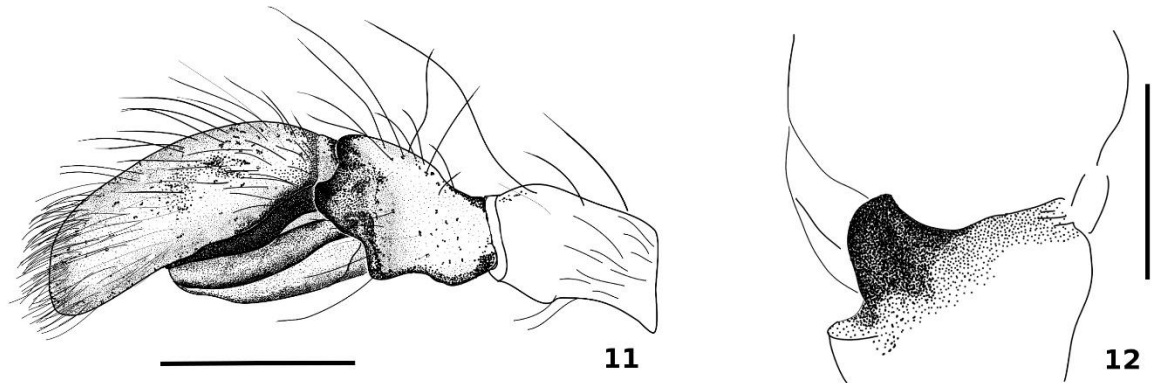
Figures 5 – 7

Hypaeus olympeae **sp. nov.** left male palp; 5. retrolateral view; 6. Same ventral view; 7. Same dorsal view showing tibial apophysis, scale 0,5mm.



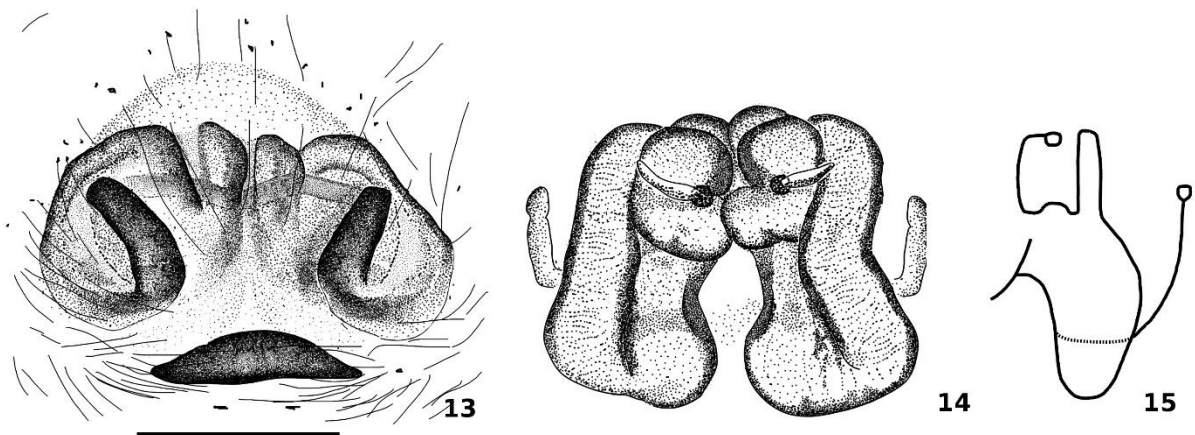
Figures 8 – 10

Hypaeus olympeae **sp. nov.** female; 8. epigyne, ventral view; 9. same, cleared; 9. ventral view, cleared, scale 0,5mm.



Figures 11 – 12

Hypaeus olympeae **sp. nov.** left male palp drawings; 11. retrolateral view; 12. same, dorsal view showing tibial apophysis, scale 0,5mm.



Figures 13 – 15

Hypaeus olympeae **sp. nov.** female; 13. Epigyne drawing; 14. same ventral view; 15. path within epigyne, scale 0,5mm.



Figures 16 - 17

Hypaeus olympeae **sp. nov.** pictures of alive specimens; 16. male holotype; 17. female paratype.

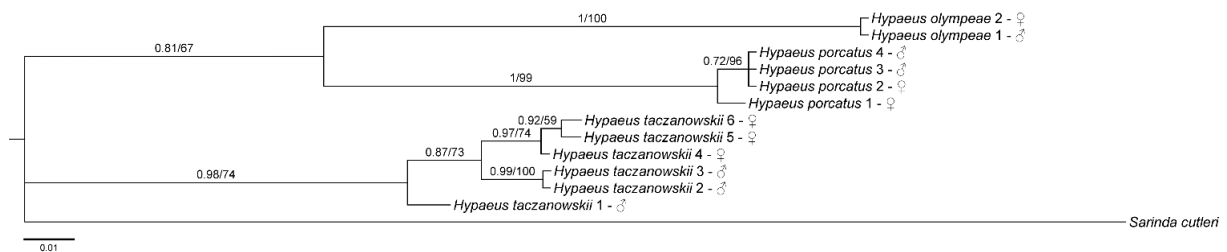


Figure 18

50% majority-rule tree from the Bayesian analysis of the COI matrix. Numbers above each branch are bootstrap values > 50% followed by posterior probabilities from the Bayesian analysis. Branch lengths are proportional to the number of substitutions per nucleotide position (scale bar = 0.01 substitutions). See Table 1 for complete voucher information.

Differential diagnosis

Males of *Hypaeus olympeae* **sp. nov.** are similar to those of *H. miles* Simon, *H. femoratus* Araújo & Ruiz and *H. terraemediae* Araújo & Ruiz for having dilated femora (Fig 4). However, *H. olympeae* **sp. nov.** has wider rounded TA, with one is small and pointed in *H. miles*, *H. femoratus* and *H. terraemediae*. Females of *H. olympeae* **sp. nov.** are similar to those of *H. femoratus* and *H. terraemediae* (the female of *H. miles* is unknown). Digitiform glands curve from the center of the epigyne to the anterio lateral portion. Females of *H. olympeae* **sp. nov.** are slightly similar in shape to those of *H. femoratus* and *H. terraemaediae* but the copulation openings are less curved and space between them is bigger.

Etymology

The species is named *olympae* to pay tribute to Olympe Delavalle, daughter of the Curator of the NNR Nouragues during our survey.

Material examined

Holotype

Male from RNN des Nouragues (4°02'N, 52°41'W), Camp Pararé, French Guiana, 11.XII.2013, Cyril Courtial (AR 16169).

Paratypes

One female from RNN des Nouragues (4°02'N, 52°41'W), Camp Pararé, French Guiana, 11.XII.2013, Cyril Courtial (AR 16170); one male, two females from RNN de la Trinité (04°36'N, 53°24'W), Camp Aya, French Guiana, 08.XII.2010, Alain Canard.

Additional material examined

French Guiana. RNN de la Trinité, Camp Aya (04°36'N, 53°24'W): 1♂, 01.XI.2008, Frédéric Ysnel ; RNN des Nouragues, Camp Inselberg (4°05'N, 52°41'W): 1♀, 09.XII.2013, Cyril Courtial ; RNN des Nouragues, Camp Pararé (4°02'N, 52°41'W): 1♀, 26.VI.2010, Vincent Vedel ; Montagne des Chevaux (4 43'N, 52 24'W): 1♀, 09.XI.2010, Vincent Vedel ; Roche Bénitier (04°36'N, 53°24'W) : 1♀, 06.IV.2010, Vincent Vedel.

Description

Male (Holotype, AR 16169)

Total length: 6.00. Carapace dark brown with light spot behind the fovea bearing white setae (Fig 1), 3.10 long, 2.30 wide, 1.80 high. Occular quadrangle 2.00 long. Anterior eye row 2.20 wide, posterior 2.00 wide. AME 0.70 in diameter. Clypeus 0.45 high. Chelicera dark brown (Fig 3) with short mastidions pointed forward; 3 posterior cheliceral teeth, 2 anterior cheliceral teeth. Palp: femur curved with dorsal bump (Fig 4); tibia with quiet short rounded RTA (Figs 5, 7, 11-12); embolus emerging from proximal tegulum with median portion slightly narrowed (Fig 6). Legs 1342 (10.00/6.90/7.80/7.50). Length of femur I 2.80, II 2.20, III 2.60, IV 2.40. Patella + tibia I 4.30, II 2.70, III 2.70, IV 2.40. Metatarsus + tarsus I 2.90, II 2.00, III 2.50, IV 2.70.

Abdomen pale with median longitudinal light stripe (Figs 1, 16) and ventrally with median longitudinal dark brown stripe. Spinnerets light brown.

Variation Male (n=3)

Total length: 6.00-7.10. Carapace length: 3.05-3.20. Length of leg I 9.05-10.00.

Female (AR 16170)

Total length: 9.00. Carapace light brown with darker cephalic area, base of the cephalothorax bearing dark spots (Fig 2), 3.90 long, 2.70 wide, 2.00 high. Occular quadrangle 1.90 long. Anterior eye row 2.40 wide, posterior 2.10 wide. AME 0.80 in diameter. Clypeus 0.30 high. Chelicera dark brown with no mastidion; 3 posterior cheliceral teeth, 4 anterior cheliceral teeth. Legs 1-432 (8.60/8.60/8.40/6.90). Length of femur I 2.60, II 2.30, III 2.90, IV 2.90. Patella + tibia I 3.70, II 2.80, III 3.00, IV 3.00. Metatarsus + tarsus I 2.30, II 1.80, III 2.50, IV 2.80. Epigyne with a pair of oblique copulation openings, long digitiform gland ducts and long and thin copulation ducts.

Variation Female (n=6)

Total length: 6.20-9.00. Carapace length: 2.70-3.90. Length of leg I 7.30-8.60.

Distribution

Only known from French Guiana.

Comments

Type specimen and paratype were caught during mating behaviour in a building at the Nouragues field station.

DNA sequences and phylogenetic analysis.

The COI alignment was 442 base pairs (bp) long and included 92 variable sites of which 72 were informative in parsimony. The BI and ML topologies are congruent; there was no topological conflict detected between the 50% Bayesian majority-rule consensus tree (Fig. 18) and the ML bootstrap 50% majority-rule consensus tree (not shown). The topology we obtained showed (1) that the two individuals of *H. olympeae* **sp. nov.** included in the study form a strongly supported monophyletic grouping (PP = 1; BS = 100), highly divergent from the two other clades in the tree, (2) that the four accessions sampled for *H. porcatus* are part of a strongly supported clade (PP = 1; BS = 99) resolved as sister to *H. olympeae* **sp. nov.** but with poor support (PP = 0.81; BS = 67) and (3) that the 6 accessions identified as *H. taczanowskii* (3 male and 3 female individuals) were all included in a monophyletic grouping strongly supported in BI (PP = 0.99; BS = 74). The analysis of COI sequences then confirms the current morphological circumscriptions for the three *Hypaeus* species sampled here. Also, the branch lengths observed between the three clades recognized here are relatively high when compared with the magnitude of the divergence between the ingroup (viz. genus *Hypaeus*) and the outgroup (viz. *Sarinda cutleri*); this further supports the recognition of *H. olympeae* **sp. nov.** as a distinct species.

Addition to the French Guiana's jumping spiders' list

According to Vedel *et al.* (2013), Courtial *et al.* (2014) and Logunov (2015) we add nine new species for French Guiana.

Eustiromastix moraballi Mello-Leitao, 1940

RNN Nouragues, camp Pararé (4°02'N, 52°41'W), 1♂, 06.XII.2013, Canard Alain, Courtial Cyril, Leroy Boris, Pétilion Julien & Vedel Vincent, at sight in low vegetation.

Lyssomanes tenuis Peckham & Wheeler, 1889

RNN Nouragues, camp Inselberg (4°05'N, 52°41'W), 1♂, 08.XII.2013, Courtial Cyril, by beating by beating the lower branches of trees.

Scopocira abaporu Costa & Ruiz, 2014

Nouragues, Camp Pararé (4°02'N, 52°41'W), 1♂, 13.XII.2013, Courtial Cyril, by beating the lower branches of trees.

Scopocira histrio Simon, 1900

Nouragues, camp Inselberg (4°05'N, 52°41'W), 1♀, 10.XII.2013, Courtial Cyril, by beating the lower branches of trees. Nouragues, camp Pararé (4°02'N, 52°41'W), 1♂, 06.XII.2013, Canard Alain, Courtial Cyril, Leroy Boris, Pétilion Julien & Vedel Vincent, by beating the lower branches of trees.

Colonus germaini Simon, 1900

Nouragues, camp Pararé (4°02'N, 52°41'W), 1♀, 12.XII.2013, Courtial Cyril, by beating the lower branches of trees.

Corcovetella aemulatrix Galiano, 1975

Kourou, degrad saramak (5°01'N, 52°41'W), 1♀, collection date unknown, Vedel Vincent, by beating vegetation in garden near primary forest.

Pachomius nigrus Caporiacco, 1947

RNN Trinité, camp Aya (04°36'N, 53°24'W), 1♂, X.2010, Canard Alain, Courtial Cyril, Leroy Boris & Ysnel Frédéric, by beating the lower branches of trees.

Gypogyna forceps Simon, 1900

After examination of species described by Caporiacco (1954) deposited in the MNHN, the type species of *Cyllodania fasciata* (Caporicaco, 1954), considered as a subadult by Caporiacco (1954) and Galiano (1977) is in fact an adult female of *Gypogyna forceps* Simon, 1900 (Caporiacco, 1954: 150, f.48, French Guiana, Saint-Jean du Maroni, 1914, Benoist *leg*). *Cyllodania fasciata* (Caporicaco, 1954) is here presented as a new synonym of *Gypogyna forceps* Simon, 1900.

Kourou, degrad saramak (5°01'N, 52°41'W), 1♀, collection date unknown, Vedel Vincent, by beating vegetation in garden near primary forest.

Marma nigritarsis (Simon, 1900)

Saül (3°37'N, 53°12'W), 1♂, 08.X.2013, 1♂, 18.X.2013, Bellanger Yannick (Asper Society).

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ANNEXE.4

Les araignées exogènes modifient les assemblages trouvés dans les kipuka, fragments de forêts Hawaïien, dans l'espace et le temps

Non-native spiders change assemblages of Hawaiian forest fragment kipuka over space and time

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Abstract

We assessed how assemblages of spiders were structured in small Hawaiian tropical forest fragments (Hawaiian, *kipuka*) within a matrix of previous lava flows, over both space (sampling kipuka of different sizes) and time (comparison with a similar study from 1998). Standardized hand-collection by night was carried out in May 2016. In total, 702 spiders were collected, representing 6 families and 25 (morpho-)species. We found that the number of individuals, but not species richness, was highly correlated with the area of sampled forest fragments, suggesting that kipuka act as separate habitat islands for these predatory arthropods. Species richness was significantly lower in the lava matrix outside the kipuka compared to the kipuka habitats, although there was no statistical difference in species composition between the two habitats, largely because of similarity of non-native species in both habitats. Over the last 20 years, the abundance of non-native spider species substantially increased in both kipuka and lava habitats, in marked contrast to the vegetation that has remained more intact. With endemism of terrestrial arthropods reaching over 95% in native forests, non-native predatory species present a critical challenge to the endemic fauna.

Key-words: Araneae; diachronic study, island.

Introduction

Kipuka are small tropical forest fragments surrounded by recent lava flows on Hawaiian islands. Many of these kipuka are rich ecosystems that have been previously investigated for their importance for native passerine birds, plants (trees and ferns) and picture-winged flies (e.g. Muir & Price 2008). Due to their spatial arrangement in a volcanic matrix, kipuka can be considered as islands within islands (Tielens et al. 2019), and thus consequently important, and original, to test classical assumptions regarding the combined effects of area and isolation on species assemblages.

The kipuka system might also be used to examine whether such particular habitats retain a strong biotic resistance to non-native species. In Hawaii, due to the remote localization of this archipelago, there are well known impacts of non-native species, with most of these studies focusing on changes in ecosystem structure (e.g. Krushelnycky & Gillespie 2008). Indeed, multiple ecological impacts of non-native flora and fauna threaten communities world-wide, and can be potentially even damaging to island systems (Vitousek 1988). Although some non-native species are reported from kipuka (e.g., rats and other mammals), kipuka appear to be less vulnerable to non-native than other (lowland) habitats, with, for example, non-native plant species almost entirely absent from kipuka (Flaspohler et al. 2010). To the best of our knowledge, no study has yet assessed how non-native spiders colonized kipuka, although they represent a major group of predators in this habitat, potentially reducing native populations.

In this study, we examined how assemblages of spiders are structured over space (e.g., comparisons across kipuka as well as lava matrix), but also potentially changed over time (in comparison to a previous study during the 1990s in the same study site: Vandergast & Gillespie 2004). We tested the general hypothesis suggested by observations of relatively intact native biota (Krushelnycky & Gillespie 2008, Flaspohler et al. 2010), that kipuka function as islands with strong biotic resistance to arthropod non-native species. More precisely, our expectations are that 1) abundance and species richness increase with increasing kipuka area, 2) species composition and richness differ between kipuka habitat and the surrounding areas and 3) despite an overall increase in non-native spider species over the last decades, the increase being less in kipuka habitats than outside.

Materials and methods

Study site and collecting

Fieldwork was conducted on the youngest and largest island of the Hawaiian Archipelago, Hawaii or the Big Island. The Kipuka system investigated consists of forest fragments surrounded by an 1855-1856 lava flow originating from Mauna Loa Volcano (19°40'01"N 155°20'56"W). These forest fragments grow on 3,000-5,000 years BP soil (Vitousek 2004), range in age from approximately 750-1,500 year BP and were most likely connected before the 1855-1856 flow that currently surrounds them (Trusdell & Lockwood 2017). These kipuka

occur within the State of Hawaii Forest Reserve System (Upper Waiakea Forest Reserve), along the Daniel K. Inouye Highway (formerly Saddle Road; mile marker 16-18, Kaumana Trail).

The forest fragments' plant species composition is relatively constant across forest fragments (Raich *et al.* 1997) and is categorized as mesic to wet *ohia* (*Metrosideros polymorpha*, Myrtaceae) forest (Jacobi & Warshauer 1990). Soil characteristics are also quite constant across fragments (Raich *et al.*, 1997) but soil nutrient conditions may vary (Vannette *et al.* 2016). Surrounding these fragments, the lava matrix is a rough textured patchwork of undulating mounds of smooth lava and free chunks of very angular pieces, extremely porous where the vegetation is sparser and poorer than those of the fragments (for a detailed description of both habitats, see Vandergast & Gillespie, 2004; Flaspohler *et al.*, 2010; Vaughn *et al.*, 2014).

Vegetation-dwelling assemblages of spiders were collected in May 2016 in the kipuka fragments and outside, in the surrounding lava, of five small (<1 ha) and five large forest patches (2-11 ha). along the Saddle Road (mile marker 16-18: Kaumana trail). The influence of kipuka area on both species richness and abundance of spiders was tested using linear regressions. Kipuka area was estimated using airborne LiDAR (Light Detection and Ranging) technology as reported by Flaspohler *et al.* (2010).

Field collection involved beating vegetation at night, the best time for collecting spiders. Each kipuka and surrounding lava was sampled by 2 people for a total of 30min, a time determined following initial sampling. Individuals were collected in separately in ethanol for identification to species or morpho-species (i.e., spider family) level at the lab. During identification, specimens were checked against voucher specimens obtained/used in the previous study (Vandergast & Gillespie, 2004). All specimens are stored at the University of Rennes, France.

Data analysis

The influence of kipuka size on both species richness and abundance of spiders was tested using linear regressions. Paired T-tests and Permanova (1000 permutations) were used to test for differences in species richness and composition, respectively, between the two habitat types. Non-metric multi-dimensional scaling ordination was used to visualize spider assemblages in the two habitats. 'Indigeneity status' was assessed using multiple bibliographic sources (see details in Vandergast & Gillespie, 2004), combined with the expertise of one of the authors (RG). Proportion of native vs non-native species were compared between kipuka and lava habitats in the same area in 2016 in 1998 (from Vandergast & Gillespie, 2004) using χ^2 tests. To allow a direct comparison of kipuka and lava habitats with previous sampling we pooled the two kipuka sampling categories of "core" and "edge" reported in the earlier study.

Results

In total, 702 spiders belonging to 6 families and 25 (morpho-) species were collected (see details in Table 1).

Table 1 : Number of individuals, status (Na=Native, Nn=Non-native, *: species not found in 1998, according to Vandergast & Gillespie 2004) and code of spider taxa collected inside and outside the kipuka.

Family	Genus	species	Status	Nind (kipuka)	Nind (lava)	Code
Araneidae	<i>Cyclosa</i>	<i>sp.</i>	Na	21	51	Cycsp
	<i>Neoscona</i>	<i>sp1</i>	Nn	42	1	Neosp1
	<i>Neoscona</i>	<i>sp2</i>	Nn*	23	31	Neosp2
Linyphiidae	<i>Agyneta</i>	<i>sp.</i>	Nn*	3	0	Agysp
Miturgidae	<i>Cheiracanthium</i>	<i>sp.</i>	Nn*	1	13	Chesp
Philodromidae	<i>Pagiopapulus</i>	<i>sp.</i>	Na*	4	0	Pagsp
Tetragnathidae	<i>Tetragnatha</i>	<i>acuta</i>	Na	56	85	Tetac
	<i>Tetragnatha</i>	<i>anuenue</i>	Na	43	44	Tetan
	<i>Tetragnatha</i>	<i>brevignatha</i>	Na	26	0	Tetbr
	<i>Tetragnatha</i>	<i>hawaiiensis</i>	Na	21	0	Tetha
	<i>Tetragnatha</i>	<i>quasimodo</i>	Na	27	6	Tetqu
	<i>Tetragnatha</i>	<i>spp.</i>	Na	2	0	Tetsp
Theridiidae	<i>Argyrodes</i>	<i>sp.</i>	Na	1	0	Thesp7
	<i>Ariamnes</i>	<i>spp.</i>	Na*	59	1	Argsp
	<i>Steatoda</i>	<i>grossa</i>	Nn*	11	0	Stegr
	<i>Theridion</i>	<i>grallator</i>	Na	20	0	Thegr
	<i>Theridion</i>	<i>sp1</i>	Na	23	35	Thesp1
	<i>Theridion</i>	<i>sp2</i>	Na	8	2	Thesp2
	<i>Theridion</i>	<i>sp3</i>	Na	1	0	Thesp3
	<i>Theridion</i>	<i>sp4</i>	Na	4	2	Thesp4
	<i>Theridion</i>	<i>sp5</i>	Na	4	6	Thesp5
	<i>Theridion</i>	<i>sp6</i>	Na	2	3	Thesp6
Thomisidae	<i>Mecaphesa</i>	<i>sp1</i>	Na*	1	3	Mecsp1
	<i>Mecaphesa</i>	<i>sp2</i>	Na*	4	10	Mecsp2
	<i>Synaema</i>	<i>sp.</i>	Na*	1	1	Synsp

Kipuka size had a large effect on the number of individuals (linear regression, $Y = 5.58X(\text{ha}) + 27.4$, $R^2 = 0.93$, $p < 0.001$, 9df), but no effect on species richness (linear regression, $R^2 = 0.12$, NS, 9df). Species richness of spiders was significantly higher in kipuka habitats compared to the surrounding lava (mean \pm se: 10.8 ± 0.6 vs. 6.8 ± 0.6 respectively; Paired T-test, $t = 6.34$, 9 df, $p < 0.001$), although there was no statistical difference in species composition between the two habitat types (Permanova: $F_{1,8} = 0.06$, $p = 0.349$, Fig. 1). The proportion of non-native spider species increased significantly between 1998 and 2016, in both kipuka and lava habitats (χ^2 tests, $\chi^2 = 67.53$, 1 df, $p < 0.001$ and $\chi^2 = 4.34$, 1 df, $p < 0.037$ respectively), with a higher increase in kipuka habitats (see Fig. 2). This increase in both habitat types was due to both an increase in the number of non-native species and a particular increase in the number of individuals of few species (e.g. *Steatoda grossa*: Table 1).

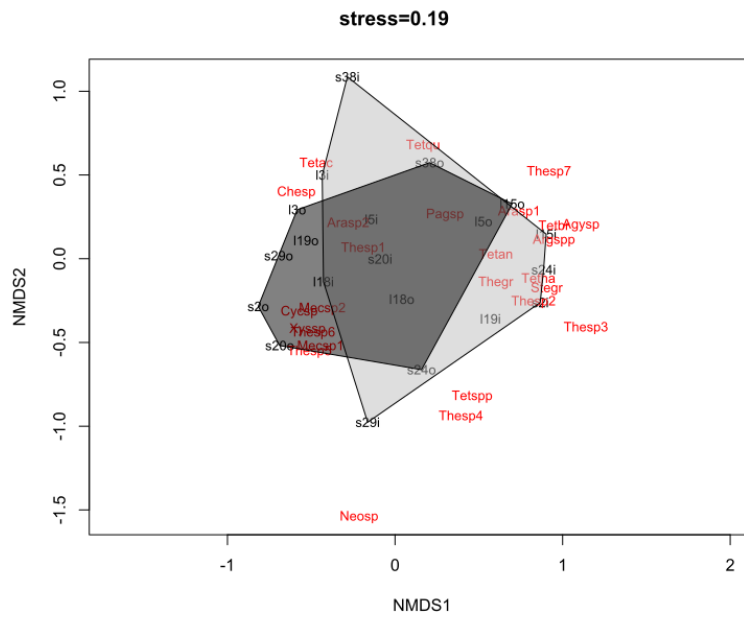


Figure 1 : Non-metric multi-dimensional scaling ordination of spider assemblages from kipuka habitats (grey ellipsoid) and surrounding lava (black ellipsoid). Species are in red and sampling stations in black. Stress=0.189.

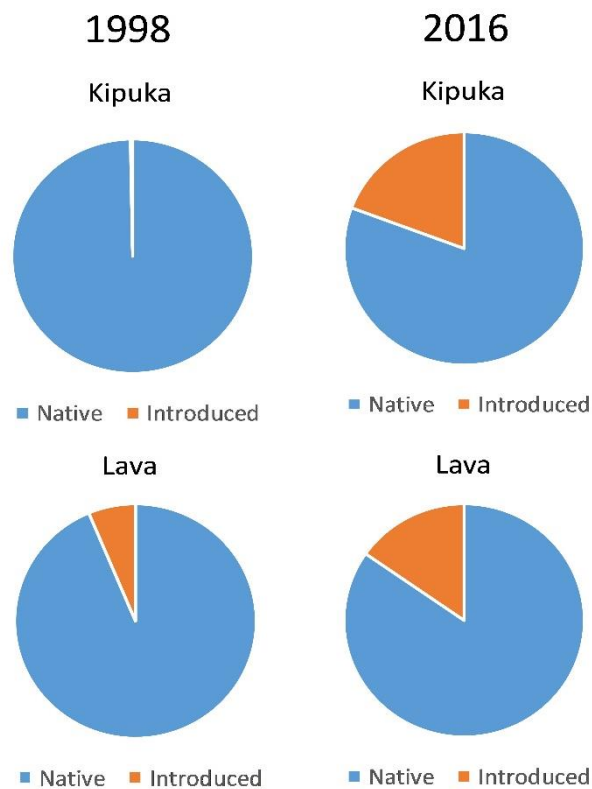


Figure 10 : Relative abundance of native (blue) and non-native (orange) species in kipuka habitats and surrounding lava, in 1998 (430 individuals) and in 2016 (702 individuals). For spider taxa code, see Table 1.

Discussion

The total number of individuals across all spider species was strongly associated with the area of sampled forests, suggesting that kipuka act, at least partly, as separate habitat islands for the spiders. Yet, as recently observed for entire arthropod communities in the same area (Tielens et al. 2019), spider species richness was not a function of kipuka size. Indeed, spider species in kipuka habitats tend to be found in all such habitats (Vandergast & Gillespie 2004, Vandergast et al, 2004). These two results altogether suggest that kipuka act as islands for native species in a hostile matrix. Yet, the abundance of several native and non-native species was found to be high in both kipuka habitats and surrounding lava, leading to overlapping, and statistically indistinguishable, assemblage compositions (see also Tielens et al. 2019). Fragment size is known to be a strong determinant of the structure of the forest in the kipuka (Vaughn et al., 2014) with larger fragments having greater average height, larger diversity of height and lower edge to core habitat being thus less affected by the matrix overall. Kipuka edges are also known to house different species from the kipuka interiors (Vandergast & Gillespie 2004). For example, more native *Drosophila* are found in large kipuka while more non-native *Drosophila* and other insects are found in small kipuka (Mueller 2015). Patch size, on top of influencing habitat quality, is also known to act on migration rates, and the linear relationships between kipuka area and number of spider individuals can be also be the result of immigration-emigration dynamics (Hambäck & Englund 2005).

There was an important increase in the proportion of non-native species over time, while no native species disappeared between the two sampling periods. Several new species like *Cheiracanthium* sp. and *Steatoda grossa* were detected in this study, i.e. they were not recorded in the same study site twenty years ago. Other species have an unclear biogeographic and taxonomic status, e.g. *Agyneta* sp., which shows that more intensive studies are still needed on the Hawaiian archipelago (Gertsch 1973). The kipuka we sampled belong to the State of Hawaii Forest Reserve System (Upper Waiakea forest reserve), an area subject to limited anthropogenic disturbance for the last 160 years, but importantly located along the Daniel K. Inouye Highway that was reconstructed in 2008 and 2011. Thus, the increase of non-native species is likely associated with previous construction activity and more road traffic along the renovated highway. Non-native arthropods in Hawaii respond more quickly to disturbance than their endemic counterparts (Gillespie et al, 2008) and are known to follow pathways of human activity (Krushelnycky & Gillespie 2008). Interestingly, the increase in non-native spiders was actually higher in kipuka habitats compared to the outside lava, rejecting our hypothesis of a stronger biotic resistance to non-native species in intact forest fragments, and in marked contrast to the relatively intact flora of these habitats. Kipuka offer many micro-habitats for new comers, for example, bark of *Metrosideros polymorpha* where *Steatoda grossa* are often found in numbers, as well as complex edge habitats where one species of non-native spiders was found previously (Vandergast & Gillespie 2004).

In conclusion, kipuka function as habitat islands within islands, with many island-like features such as a characteristic biota, unique microclimate, and biological associations with

increasing area. Kipuka, likely other islands also appear to be vulnerable to non-native species, especially compared to surrounding lava habitats. Until now native species of spiders do not seem affected by these new comers, but spiders can have a large impact on prey species because they are ecologically dominant and generalist predators in a large variety of habitats (Pekár & Toft 2015), including tropical forests (Coddington et al. 2009). In Hawaii, with a large number of endemic species (Howarth 1990, Eldredge and Evenhuis 2003), non-native spiders are a critical challenge for management. The impact of these new generalist predators on the structure and functioning of kipuka is currently investigated using meta-barcoding and NGS techniques. We are also planning to look at other spider associates, including parasite occurrence in spiders (see Vandergast & Roderick 2003), to see how the associated community has changed together with increased non-native species.

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- 2015** How diverse is tropical biodiversity? Standardised comparison of tropical and temperate spider assemblages and insight of molecular approach in species richness study – MSc internship (6 months), team Biodiversity and landscape management, EA 7316, University of Rennes.
with J. Pétilion & F. Ysnel
- 2014** Ecological and methodological analysis of spider assemblages of Les Nouragues Nature Reserve, French Guiana – MSc internship (3 months), team Biodiversity and landscape management, EA 7316 University of Rennes.
with J. Pétilion & F. Ysnel

PEER-REVIEWED PUBLICATIONS

1. Keller J. Imperial J., Ruiz T., **Privet K.**, Lima O., Salmon A., Aïnouche A. and F. Cabello-Hurtado (2018). Sequencing and analysis of three *Lupinus* nodulome provides new insight on the specific relationships with compatible and non-compatible *Bradyrhizobium*. *Plant Science*, **266**, 102-116.
2. **Privet K.**, Courtial C., Decaëns T., Djoudi E.A., Vedel V., Ysnel F. and J. Pétillon (2018). Spider community structure in a neotropical rainforest-inselberg complex : ecological and methodological insights from a small-scale intensive survey. *Journal of Tropical Ecology*, **59**, 21-34.
3. **Privet K.**, Vedel V., Fortunel C., Cerdan A., Martinez Q., Barraloto C., Petitclerc F., Orivel F. & J. Pétillon (2020). Relative efficiency of pitfall trapping vs. hand-collecting along a structural gradient of neotropical habitats. *Diversity*, **12**, 81 (special issue "Systematics and Evolution of Spiders").
4. Pétillon J., **Privet K.**, Vandergast A., Gillespie R. and D. K. Price (2020). Changes in spider assemblages of Hawaiian forest fragments over space and time. *Neobiota*, **55**, 1-9.
5. **Privet K.**, and J. Pétillon (2020). First quantification of the difference in spider diversity between tropical vs. temperate forests. *Ecology and Evolution*, **10**, 13165– 13172.
6. Lowe E., Wolff J., ... **Privet K.**, ... and M. Herberstein (2020). Towards establishment of a centralized spider traits database. *Journal of Arachnology*, **2**, 103-109.
7. Pekár S., Wolff J., ..., **Privet K.**, ..., E. Lowe. The World Spider Trait Database (WST): a centralised global open repository for curated data on spider traits. *Database*, **2021**, baab064.
8. Courtial C., **Privet K.**, Picard L. and J. Pétillon. Description of new species of *Hypaeus* Simon (Araneae, Salticidae, Amycinae) based on integrative taxonomy. Submitted to *Studies on Neotropical Fauna and Environment*.
9. **Privet K.**, Chao A., Hamrik T., Lamarre G, and J. Pétillon. Complementary of taxon- and trait-based metrics to understand tropical diversity – A case study using spider assemblages of Neotropical forests habitats. *In prep*.
10. **Privet K.**, Pétillon J., Rosemary G., and H. Krehenwinkel. Phylogenetic relationships among Hawaiian wolf spiders suggest recent radiation influenced by the adaptation to different environments. *In prep*.
11. Lalagüe H., Fortunel C., **Privet K.**, Védél V. and J. Pétillon. Unexpectedly high contribution of vertical vs. horizontal strata to spider diversity in Amazonian forests. *In prep*.

COMMUNICATIONS

1. **Privet K.**, and J. Pétillon (2018). Differences in tropical vs. temperate diversity in arthropod predators provide insights into causes of latitudinal gradients of species diversity. *International Conference on Ecological Sciences*, October 22-25 2018, Rennes (France).
2. Pétillon J., **Privet K.**, Vandergast A., Gillespie R. and D. Price (2018). Drivers of spider assemblages in Hawaiian forest fragments (Kipuka). *International Conference on Ecological Sciences*, October 22-25 2018, Rennes (France).
3. **Privet K.** & J. Pétillon (2019). Comparative patterns of taxonomic-, phylogenetic- vs. functional-based diversity metrics at small and large spatial scales. *Spider traits workshop*, February 10 2019, Christchurch (New-Zelände).
4. **Privet K.**, Krehenwinkel H., Gillespie R. and J. Pétillon (2019). Phylogeny of the wolf spiders from the island of Hawai'i inferred from multilocus genetic data. *21st International Congress of Arachnology*, February 11-15 2019, Christchurch (New-Zelände).
5. Pétillon J., **Privet K.**, Fortunel C., Cerdan A., Martinez Q., Barraloto C., Petitclerc F., Orivel F. & V. Vedel (2019). Relative efficiency of pitfall trapping vs. hand-collecting along a structural gradient of neotropical habitats. *21st International Congress of Arachnology*, February 11-15 2019, Christchurch (New-Zelände).
6. **Privet K.**, Pétillon J., Gillespie R. and H. Krehenwinkel (2021). Phylogeny of wolf spiders from the Hawaiian archipelago inferred from multilocus genetic data. *32rd European Congress of Arachnology*, August 23-26 2021, online.

GRANTS & AWARDS

International Society of Arachnology Student Travel Grant 2019 – Travel grant to assist and present at the 21st International Congress of Arachnology, 2019 in New Zealand (Christchurch).

American Arachnological Society Student Research Grant 2020 – Travel grant to do field work in Hawaii, USA in 2021.

Rennes' Doctoral School Mobility Grant 2021 (Cancelled due to Covid-19 restrictions)– Travel grant to visit Dr. Megan Porter at the Department of Biology the University of Hawai'i at Manoa.

SUPERVISION

Marti S.L., 2020. Development of molecular analysis methods on museum spider specimens – Assistant engineer (5 months), Ecobio, UMR CNRS / University of Rennes

Berlier L., 2019. Functional and phylogenetic diversity of spiders in tropical forests of French Guiana – 3rd year Bachelor student (4 months), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétillon

Poirier A., 2019. Functional diversity of spiders from the main tropical forest habitats of the Amazon basin – 1st year Master student (3 months), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétillon

Salomon L., 2019. Functional diversity of spiders from the main tropical forest habitats of the Amazon basin – 2nd year Bachelor student (1 month), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétillon

Le Naviel A., 2018. Small and large-scale variation in spider diversity of major tropical forest habitats in French Guiana – 1st year Master student (3 months), Ecobio, UMR CNRS / University of Rennes. Co-supervisor: J. Pétillon

Hacala A., 2016 Specific and functional diversity of spiders across tropical forest gradient in French Guiana – 1st year Master student (3 months), Team Biodiversity and Landscape management, EA University Rennes. Co-supervisors: C. Courtial et G. Lamarre.

SYNERGISTIC ACTIVITIES

- **PhD representative in the Lab Advisory council** – 2017-2019
- **Member of the Training committee of the Doctoral school EGAAL**–2018-2019
- **Main organizer of the symposium “Island Arachnids Biogeography”** – 21st International Congress of Arachnology, Christchurch, February 2019, co-organizers: Julien Pétillon, Rosemary Gillespie and Sarah Boyer.
- **Member of the International Society of Arachnology, the American Arachnological Society and the European Society of Arachnology** – since 2017
- **Member of the British Ecological Society** – since 2017
- **Member of the Australasian Arachnological Society and the Society for the study of Evolution** – since 2019
- **Member of the Society for the Study of Evolution** – since 2019

Titre : Facteurs multi-échelles structurant les diversités en taxons, traits et unités évolutives des araignées en milieux tropicaux

Mot clés : communautés, filtrage d'habitat, forêts Néotropicales, Hawaii, Lycosidae, phylogénie

Résumé : Décrire les patterns de diversité biologique et comprendre leurs origines est l'un des principaux défis de l'écologie moderne. En particulier, les milieux tropicaux sont les écosystèmes terrestres les plus riches en espèces et parmi les moins bien connus. Les araignées constituent un groupe modèle pertinent en écologie, car elles sont abondantes et diverses, avec une grande importance écologique, et dont l'étude devrait permettre de mieux comprendre les processus responsables des patterns de diversité. Nous avons étudié les patterns de diversité et les processus responsables des assemblages d'araignées dans les forêts Néotropicales et dans l'archipel d'Hawaï en utilisant un ensemble d'approches complémentaires (basées sur les taxons, les traits, les unités évolutives). En raison du manque de connaissances sur l'échantillonnage et la diversité des araignées tropicales, nous avons testé et comparé différentes méthodes d'échantillonnage et protocoles standardisés en nous concentrant sur différentes strates de végétation. Nous avons développé une base de données morpho-espèces pour pallier le manque de connaissances taxonomiques. Nous avons

étudié un ensemble de traits (taille du corps, longueur des pattes et guildes de chasse) afin de tester leur caractère informatif pour les assemblages tropicaux. Enfin, nous avons déterminé des unités évolutives pour étudier la diversité en appliquant une approche multilocus (mitochondriale et nucléaire) sur une grande collection d'araignées tropicales, pour lesquelles les connaissances taxonomiques sont incomplètes et problématiques. Nous avons montré que les patterns de diversité des taxons, des traits et des unités évolutives des araignées tropicales sont influencés par l'habitat, et que par conséquent le filtrage de l'habitat est crucial pour déterminer les assemblages de ces araignées. En outre, nous avons montré la nature dépendante du contexte et de l'échelle des patterns de diversité des araignées tropicales avec des variations des assemblages d'araignées tropicales à une échelle plus fine que celle des habitats. Dans l'ensemble, cela plaide pour davantage d'études de cas étudiant les patterns de diversité tropicaux à l'échelle des strates, des sous-structures de végétation et des conditions de micro-habitats, pour lesquels nous suggérons des axes de recherche.

Title : Multiscale factors structuring diversity in taxa, traits and evolutionary units of spiders in tropical environments

Keywords: communities, habitat filtering, Neotropical forests, Hawaii, Lycosidae, phylogeny

Abstract : Describing patterns of biological diversity and understanding their origins is one of the major challenges of modern ecology. Tropical environments in particular are the most species-rich terrestrial ecosystems and among the least well-known. Spiders are a relevant model group in ecology, because they are abundant and diverse with high ecological importance, whose study should allow a better understanding of the processes responsible for diversity patterns. We investigated the patterns of diversity and the processes responsible for spider assemblages in Neotropical forests and the Hawaiian archipelago using a set of complementary approaches (based on taxa, traits, evolutionary units). Due to the lack of knowledge on sampling and diversity of tropical spiders, we tested and compared different sampling methods and standardized protocols by focusing on different vegetation strata. We developed a morpho-species database to overcome the lack of taxonomic knowledge. We studied a set of traits

(body size, leg length and hunting guilds) to test their informative character in tropical assemblages. Finally, we determined evolutionary units to study diversity by applying a multilocus (mitochondrial and nuclear) approach on a large collection of tropical spiders, for which taxonomic knowledge is incomplete and problematic. We have shown that the taxon-, traits- and evolutionary units diversity patterns of tropical spiders are influenced by the habitat, and that consequently habitat filtering is crucial in determining the assemblages of these spiders. In addition, we have shown the context-dependent and scale-dependent nature of diversity patterns in tropical spiders with variations of tropical spider assemblages at a finer scale than that of habitats. Overall, this plaid for more case studies studying tropical diversity patterns at the scale of strata, vegetation sub-structures, and micro-habitat conditions, for which we are suggesting research axe.