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Macroecological networks : integrating biogeography, spatial processes and species interaction networks

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Núria Galiana Ibañez. Macroecological networks : integrating biogeography, spatial processes and species interaction networks. Environmental Engineering. Université Paul Sabatier - Toulouse III, 2018. English. NNT : 2018TOU30353 . tel-02927153

HAL Id: tel-02927153

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THÈSE

En vue de l'obtention du DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par l'Université Toulouse 3 - Paul Sabatier

Présentée et soutenue par
Núria GALIANA IBAÑEZ

Le 30 octobre 2018

**Réseaux macroécologiques: intégration de la
biogéographie, des processus spatiaux et des réseaux
trophiques**

Ecole doctorale : **SEVAB - Sciences Ecologiques, Vétérinaires, Agronomiques et
Bioingenieries**

Spécialité : **Ecologie, biodiversité et évolution**

Unité de recherche :
SETE - Station d'Ecologie Théorique et Expérimentale

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UNIVERSITÉ ET LABORATOIRES

Cette thèse a été réalisée au sein du laboratoire:

Centre for Biodiversity Theory and Modelling

à la **Station d'Ecologie Théorique et Expérimentale** du CNRS

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Elle a été financée par:

Laboratoire d'Excellence TULIP de la région Midi-Pyrénées

RÉSUMÉ

La recherche sur les réseaux écologiques a identifié des motifs universels dans la façon dont les espèces interagissent entre elles, et les conséquences que cela peut avoir sur la dynamique et stabilité des écosystèmes. Les processus responsables de ces structures ont été étudiés à l'échelle locale. En revanche, l'influence de processus opérant à plus grande échelle, tels que le climat ou l'hétérogénéité des habitats, est encore très mal comprise. Il subsiste une lacune fondamentale dans notre compréhension de la manière dont les processus spatiaux et biogéographiques affectent la structure des réseaux d'interactions. L'objectif principal de cette thèse est de combler cette lacune en élaborant une vision globale des réseaux macroécologiques, intégrant réseaux écologiques et biogéographie.

Dans un premier temps, j'étudie la variation géographique de la structure des réseaux écologiques. Plus précisément, je considère la façon dont la spécialisation biotique change le long de grands gradients biogéographiques. Il est généralement admis que la spécialisation biotique augmente vers l'équateur. Cependant, des études récentes ont contesté cette vision, mais en se limitant à l'échelle locale. Dans le premier chapitre de la thèse, j'utilise un ensemble de données globales de réseaux écologiques pour montrer que le gradient géographique de spécialisation biotique n'est pas universel. Il dépend à la fois de la mesure de spécialisation biotique analysée et de l'échelle spatiale d'observation.

Dans un deuxième temps, j'étudie la manière dont la structure des réseaux change à travers les échelles spatiales. Bien que les relations aire-espèces soient essentielles pour comprendre la répartition spatiale de la biodiversité, les communautés écologiques ne sont pas de simples collections d'espèces mais forment des réseaux complexes d'interactions. Dans un monde en pleine mutation anthropogène, comprendre comment la structure de ces réseaux change avec l'aire des régions considérées est essentiel pour appréhender les conséquences écologiques de la perte d'habitat et de la fragmentation. Je développe pour cela un cadre théorique expliquant certains mécanismes sous-jacents aux changements de structure des réseaux avec le changement d'échelle spatiale. Je teste ensuite ces prédictions avec un large ensemble de réseaux écologiques empiriques issus de différents écosystèmes et biomes du globe. Je trouve en particulier, une augmentation universelle de la complexité des réseaux écologiques avec les échelles spatiales, ainsi qu'une augmentation du nombre d'espèces spécialisées, suggérant ainsi que ces dernières requièrent, pour subsister, de larges aires.

Enfin, j'implémente la biogéographie dans l'analyse du changement de structure des réseaux à travers les échelles spatiales. Pour cela, en me basant sur une vaste base de données sur les vertébrés d'Europe et leurs interactions, j'analyse la manière dont la structure des réseaux d'interactions change avec l'aire considérée dans 10 régions biogéographiques d'Europe, afin de déterminer quels sont les principaux facteurs environnementaux affectant les relations aire-réseaux. Je trouve que la variation spatiale de la température annuelle moyenne et l'hétérogénéité des habitats sont les principaux déterminants du changement structurel des communautés écologiques à travers les échelles spatiales. L'intégration des processus spatiaux et biogéographiques dans l'analyse des réseaux écologiques est un défi fondamental pour progresser vers une approche plus globale, et mieux prédire l'impact du changement climatique sur les écosystèmes, ouvrant, de surcroît, de nouvelles perspectives pour évaluer la stabilité et le fonctionnement des écosystèmes à différentes échelles spatiales.

ENGLISH TITLE:

**MACROECOLOGICAL NETWORKS: INTEGRATING
BIOGEOGRAPHY, SPATIAL PROCESSES AND SPECIES
INTERACTION NETWORKS**

ABSTRACT

Research on ecological networks has identified universal patterns in the way species interact across different habitat types and their consequences for community dynamics and stability. However, most processes responsible for the observed structural patterns are suggested to operate at the local scale. The influence of processes operating at larger scales, such as climate or habitat heterogeneity, on the structure of species interaction networks and its dynamics, is still largely unknown. A fundamental gap thus exists concerning the way spatial and biogeographical processes affect the structure of species interaction networks. The main objective of this thesis is to fill this gap by building a comprehensive view on macroecological networks that integrates ecological networks and biogeography.

First, I focus on the geographical variation of the structure of ecological networks. Specifically, on how biotic specialization changes across large biogeographical gradients of environmental constancy. Prevailing wisdom states that biotic specialization increases towards the Equator. However, recent studies have challenged this view showing non-conclusive results. A major limitation of these studies is their focus on the local scale. In the first chapter of the thesis, I use a global dataset of ecological networks to show that the geographical gradient of biotic specialization is not universal. It depends on both the facet of biotic specialization analysed and the spatial scale of observation.

Second, I study how network structure changes across spatial scales. Species–area relationships are pivotal to understand the distribution of biodiversity across spatial scales. Yet, ecological communities are not just mere collections of species but also sets of interactions between them. Understanding how the structure of the complex network of biotic interactions changes with area size is thus central to extend our knowledge on the possible effects of habitat loss and fragmentation on ecological communities in a changing world. To tackle this challenge, I first develop a theoretical framework to understand the possible mechanisms underlying the changes in network structure across spatial scales and I then empirically test the theoretical predictions with a large set of ecological networks from different ecosystems and biomes across the globe. I find a universal increase of the complexity of ecological networks across spatial scales together with an increase in the number of specialist species, suggesting that they require larger areas to be found.

Finally, I integrate ecological networks, spatial processes and biogeography by analysing the geographical variation in the spatial scaling of network structure. I analyse the changes in network structure with area size across 10 biogeographical regions in Europe to determine which are the main environmental factors affecting the shape of Network-Area Relationships (NARs). I find that the spatial variation in the mean annual temperature and habitat heterogeneity are the main determinants of the spatial scaling of ecological communities. The integration of spatial and biogeographical processes into species interaction networks is a fundamental challenge to progress towards a more comprehensive approach that helps us to better predict the effect of future scenarios of global change on our ecological systems. It opens new perspectives to assess community stability and ecosystem functioning at different spatial scales.

ACKNOWLEDGEMENTS

Una tesi mai és el resultat de l'esforç d'una sola persona, i aquesta no n'és una excepció. Tot aquest treball mai hauria estat possible sense el suport i la comprensió de totes les persones que m'han envoltat aquests darrers anys.

M'agradaria començar per agrair la paciència i dedicació del José. No ha sido un camino fácil. Gracias por confiar en mi en un inicio incierto y por transmitirme tu fascinación por la ecología y las redes de interacciones, que tantas discusiones apasionantes nos han proporcionado. Gracias por enseñarme a no dejar nunca de hacerme preguntas y potenciar mi espíritu crítico. Probar ideas y equivocarme ha sido ciertamente uno de los mejores aprendizajes. Gracias por fomentarlo.

Esta tesis se debe en gran parte a Miguel. Gracias por estar siempre. Para discutir cualquier idea, para resolver cualquier duda o para empezar cualquier nuevo proyecto que se nos ocurriera tomando café. Los pájaros de Ariège te echaran de menos. Seguro que nuestros caminos se volverán a cruzar.

Sempre estaré en deute amb el Bernat Claramunt. Gràcies per creure en mi i ajudar-me a fer els meus primers passos científics. Sens dubte, avui no seria aquí si no fos per tu. També m'agradaria mostrar el meu agraïment a totes aquelles persones que, d'una manera o d'una altra, han intervingut en la meua carrera científica. I will always be grateful to Dominique Gravel for hosting me in his lab at the very beginning of my scientific career. That summer in Rimouski was inspirational and opened many new avenues in my ecological thinking. Thanks also to Ulrich Brose, Sonia kéfi, Wilfried Thuiller and Bart Haegeman for being part of my PhD committee and sharing with me your ideas and opinions, your critical thinking and enthusiasm. I am also thankful to Anna Traveset, Bo Dalsgaard, Elisa Thébault, Jérôme Chave and Stuart Pimm for being part of my PhD jury and provide me with your insightful feedback. You made of my PhD defence, a pleasant and memorable moment. To all the people from the *Station of Ecological Theory and Experiments* in Moulis who contributed to create a great scientific environment to develop and progress as a scientist (it is too hard to move away from it!). Specially to all the members from the *Centre for Biodiversity Modelling and Theory* who truly enriched not only my ecological knowledge but also my perspective on life.

One of the best things I take from this PhD is undoubtedly all the friends I made along the way. This would not have been the same fun without all of you. With Mat, Jarard, Johannes, Jeff, Aisha and Keoni started my adventure in Moulis, which has been full of nice people sharing incredible moments and softening the harder ones. With Soraya, Azenor, Kirsten, Arielle, David, Dani, Vinicius, Matthieu, Yuval and Kevin we shared so much coffee, halva, frisbee-pizza, music, hikes. I will definitely remember our non-sensical lunch discussions with Yuval and Matthieu leading the way. Also those who passed by Moulis, Ceres and João, or Claire Jacquet with whom I shared so many (always fun) experiences. The 'hardcore' hike+climb team with Jeff, Jonathan, Agathe, Lucie, Arnaud and Fanny certainly contributed to my mental health. I am especially indebted to Jeff. I am not sure what was harder, trying to teach me everything you know about climbing or helping me understand some of your genius math tricks? Hard choice. In any case, huge thanks for countless discussions, belays and hikes in these beautiful mountains.

Tota la gent de Catalunya que des de la distància m'ha donat el seu suport i m'ha fet sentir prop de casa. Albita, Martes, Carlota, Raquel, Montse. Especialment Diego i Judith, qui en una sola trucada o un cafè em fan sentir com si no hagués marxat mai. També els companys dels màster, Pau, Mar, Maria, Maria Alba i Judit, amb qui compartim el camí de la incertesa científica. Al Carlos i la Maria José, Marta,

Genís i Anna per totes les fideuàs de diumenge. I al Biel i l'Aina per la constant explosió d'alegria que despreneu.

La família que s'escull. I és que escollir-vos és tan fàcil Pelri, Joan, Isidre, Eugeni i Uri. Perquè una abraçada és suficient per recordar el que és important de veritat. Perquè gairebé és igual de divertit descobrir el món amb vosaltres que recordar-ho després. Perquè si el riure allarga la vida, ens espera la vida eterna. Especialment tu Uri, que em dones pau i m'escalfes l'ànima. *Portes la vida als ulls*, i està plena de llum i alegria. Compartir-la amb tu és el millor regal. No em puc oblidar del Nus i la Mixina. Els millors amics d'aventures i de teràpies de relax. I per descomptat a Javi i als meu pares. Aquesta tesi és per a vosaltres. Perquè haver de repetir-vos mil vegades el títol de la tesi és insignificant al costat de tot el vostre suport i amor incondicionals. Quin privilegi de família. Gràcies de tot cor.

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GENERAL INTRODUCTION¹

Ecological communities are composed by species interacting with one another and with the environment. Much is known about how the environment influences species richness and their distribution. Little is known, however, about the influence of environmental gradients on species interactions and on the structure of the network they establish. Network structure is a key factor to understand biodiversity organization and species coexistence, and it is strongly linked to multiple ecosystem functions, such as primary productivity, biological control, pollination or ecosystem stability [1]–[4]. Understanding how network structure changes in space and across large-scale environmental gradients is, thus, fundamental to fully predict how ecological communities will behave in an increasingly changing world.

The main objective of this thesis is to incorporate spatial and biogeographical processes into ecological network research to develop of a more holistic understanding of ecological systems across spatial scales. I aim to understand how network structure changes across large geographical gradients and across spatial scales of observation, and what are the main mechanisms underlying these changes. To do so, I try to build a comprehensive view on macroecological networks that integrates ecological networks and biogeography.

In this introduction, I discuss the existent gap between two research provinces: ecological networks and biogeography. I expose the importance of both bringing a community network perspective into biogeographical studies, and adopting a gradient-based, biogeographical perspective into the study of the structure and dynamics of species interaction networks. I present some works bridging the gap between the two fields and how they help to progress toward a more comprehensive understanding of ecological communities. Finally, I argue about the importance of moving beyond the spatial scaling of species richness and understanding how the entire community (i.e., species and their biotic interactions) changes across spatial scales and the new emerging tools to do so. I conclude this introduction by outlying the different chapters that constitute the thesis. I briefly explain the focus of each of them and the main findings that contribute to the integration of networks, space and biogeography.

¹ Sections of this introduction were published as a book chapter: Montoya J.M. & **Galiana N.** (2017) Integrating species interaction networks and biogeography. In: Moore J.M., et al. (eds.), *Food Webs: Science for Impact*. Cambridge Univ. Press, pp. 289-304.

HISTORICALLY ISOLATED FIELDS: THE GAP BETWEEN ECOLOGICAL NETWORKS RESEARCH AND BIOGEOGRAPHY

The search for universalities in species interaction networks

The last fifteen years has witnessed a revolution in the study of large species interaction networks, including food webs and mutualistic networks of free-living species – as those describing plants and their pollinators (Figure 1). Numerous theoretical and empirical studies have identified universal patterns and mechanisms by which species interact across different habitat types, which in turn affect community dynamics (reviewed in [5]–[8]). These interaction patterns are not only key to understand biodiversity organization within communities, but also to predict ecosystem stability and resistance to different components of environmental change [6], [9]–[11], and important ecosystem functions, like primary production, biogeochemical cycles, pest control or pollination [1]–[4].

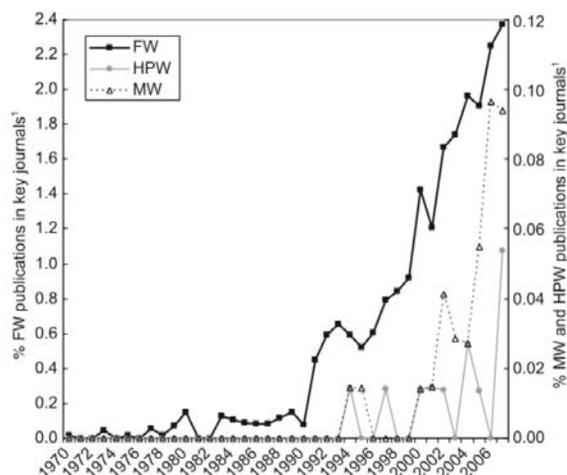


Figure 1. Annual proportion of all papers published in key journals between 1970 and 2007 that were related to ecological networks (primary axis, FW: Food webs; secondary axis, MW: mutualistic webs and HPW: host-parasitoid webs). Data were derived from searches carried out on the Web of Science data base (searched in March 2008). Figure taken from [8], where further information on the search can be found.

Although some authors warned that the idiosyncrasies of individual species and their dynamics might prevent the existence of such regularities [12]–[14], most studies suggest the existence of a few universal structural patterns in food webs and mutualistic networks [6]–[8], [15], [16]. These universalities include that most species have a few number of links to other species while only a few of them are generalists [17]–[19] (Figure 2); the existence of compartments or modules in food webs, where species

within the same compartment interact more frequently among them than with species outside of it [20]–[22], the presence of nested subsets of species in mutualistic networks, where generalists tend to interact with specialists [23], or the predominance of weak interaction strengths between consumers and their resources [24], [25].

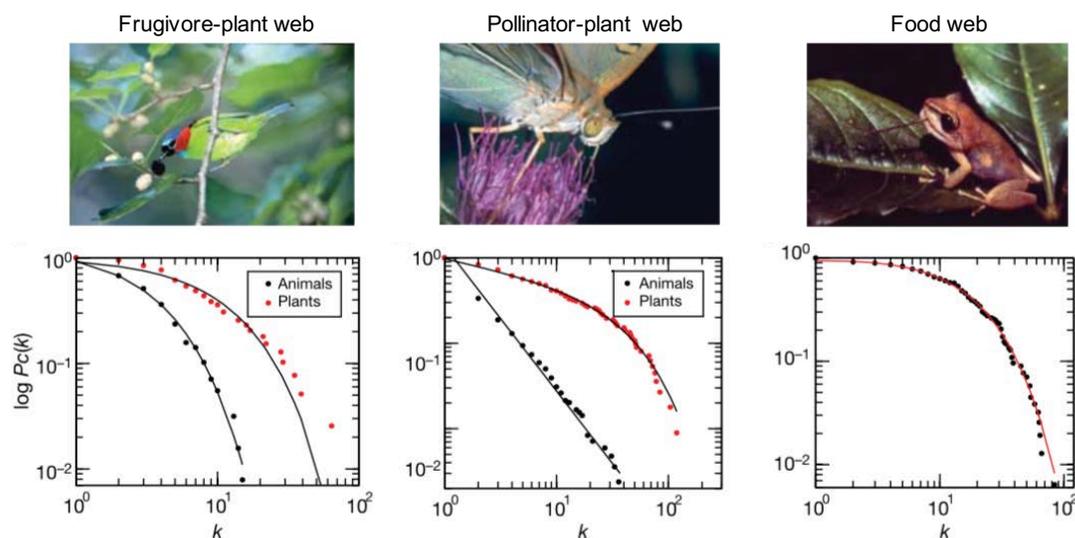


Figure 2. Characteristic degree distributions observed in different types of ecological networks. $P_c(k)$ is the cumulative probability for $\geq k$, where $P(k)$ is the probability a species has k links to other species in the network. Black lines represent the best fits and filled circles represent the empirical data. Redrawn from [6].

Most of the suggested processes responsible for these observed structural patterns and dynamics in ecological networks typically operate at the local-scale, as those related with consumer-resource dynamics, habitat occupancy or foraging behaviour. The influence of processes that operate at larger spatial extents (e.g., regional and geographical scales), such as climate or productivity, is hardly considered as a determinant of local network structure and dynamics. Notable exceptions exist. The relationships of some food web properties, like connectance and food chain length, with variables that change geographically, such as species richness, primary productivity or environmental variability, have received some attention (e.g., [15], [26]–[28]). Yet, these examples are the exception to the general rule that neglects the effects of processes operating at large spatial scales on the structure and dynamics of local communities.

Biogeography: looking for sources of geographical variability

In marked contrast to the search for universalities in networks, biogeographers (and macroecologists) look for patterns and potential processes of variation of community and species characteristics across large geographical extents. Examples include the latitudinal diversity gradient –i.e., species richness decreases with latitude [29], [30]- or the latitudinal gradient in niche breadth – i.e., niches or number of resources per consumer are narrower in the tropics ([31]–[33] but see [34]). While some biogeographers recognize the role of biotic interactions, as presented below with several examples, the majority of biogeographical studies tend to neglect the role and importance of biotic interactions [35], [36]. First, these are not considered important drivers of species distributions, with environmental variables (mostly climate) assumed to play the leading role. Second, contrary to the simultaneous consideration of multiple trophic levels and their interactions in network studies, biogeographers usually focus on “one guild at a time”, and accumulate evidence to support the observed pattern across different taxa (Table 1).

Table 1. Major conceptual and methodological differences between research on ecological networks and biogeography.

	Ecological networks	Biogeography
Spatial scale	Local-Landscape	Regional-Global
Mechanisms	Biotic interactions	Environment (Climate)
Models	Interactive population dynamics	Species occupancy and distribution
Taxonomic spread	Multiple guilds (i.e., trophic groups)	Isolated guilds
Emerging issues	Universal patterns	Variability across environmental gradients

However, it is clear that the importance of biotic interactions varies across geographical areas. It is well known that a wide range of interactions are more important at low latitude systems, including higher herbivory and insect predation in the tropics, and the predominance of tropical mutualisms such as cleaning symbioses in marine systems and ant-plant interactions in terrestrial ones [37]. Moreover, numerous studies regarding probably the oldest and most intensively studied biogeographical pattern [38], the latitudinal diversity gradient, hypothesize that more intense and stable biotic interactions in the tropics may explain the pattern [37]. Despite some historical and recent integrative efforts (see below), the burgeoning areas of ecological networks and biogeography rarely have been merged.

Different processes operating at different spatial scales?

A number of conceptual and methodological differences explain the absence of links between biogeography and species interaction network research (Table 1, Figure 3). The most evident is the spatial scale under consideration. Networks are commonly defined at the local or landscape scale, with processes affecting local species interactions as the main determinants of their structure, dynamics and functioning. In contrast, biogeography focuses on large-scale (regional to global) patterns, and the processes at play usually relate to environmental conditions, past and/or present. This is manifested via the main visualization tools used: graphs connecting species in networks *versus* maps depicting variability in biogeography (Figure 4).

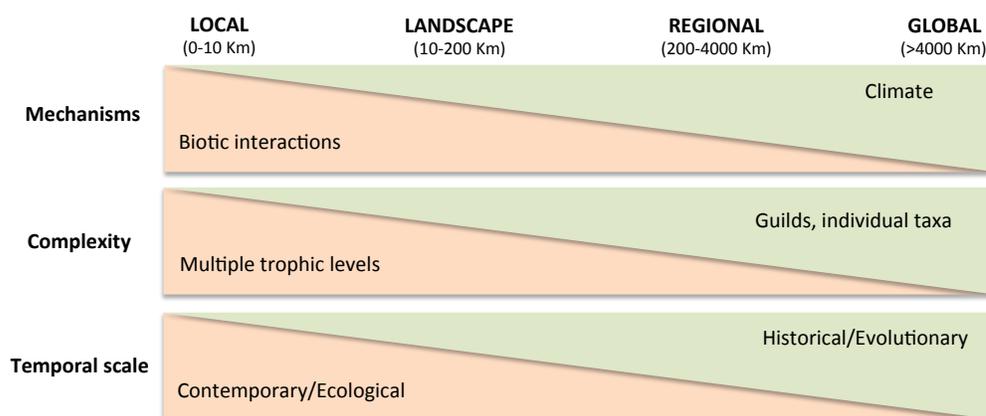


Figure 3. Variation of the relative importance of the mechanisms, level of complexity and temporal scale across the spatial scale under consideration. Local network studies typically focus on biotic interactions across multiple trophic levels over short-term temporal scales. In contrast, global/regional biogeographical studies focus on climate as the main driver within guilds and over evolutionary time scales.

The tenet is that large spatial scales are the province of climate -contemporary or past- while biotic interactions rule at local scales [39], [40]. Accordingly, Johnson [41] suggested an integrative framework for the ordering of selection processes operating across spatial scales. He identified first-order selection as the selection of physical or geographical range of species, followed by the selection of the home range of an individual or group, and finally a third- and fourth-order selection determining the feeding interactions with that individual.



Figure 4. Mapping networks. Visualization techniques greatly differ between network studies, using graphs connecting species through biotic interactions (left hand-side graphs, contrived networks), and biogeography, using maps to illustrate the analysed pattern. To determine the existence of biogeographical patterns in network structure and dynamics, we need to analyse several networks across large-scale gradients.

However, this tenet has never been tested with datasets containing detailed information on spatially explicit climatic variables and biotic interactions. In the few cases where the relative role of climate, dispersal, and biotic interactions were considered together, species interactions were actually estimated from species co-occurrence data, not from direct observations. Boulangéat and collaborators [42], for instance, used a spatially nested modelling framework to understand the distribution and abundance of plant species in the French Alps, showing that species presence-absence was determined by climatic factors and dispersal, while species abundances were mostly determined by biotic interactions, including competition and facilitation. In other words, abiotic relationships filter the species able to occupy a given environment, determining plant species composition, whereas biotic interactions manifested their importance at local scales affecting species densities. This promising approach would benefit from including observed species interactions not inferred simply from species co-occurrence data. However, such datasets for multispecies systems, and for multiple predator-prey interactions in particular, are scarce, if available at all.

Accumulating evidence suggests that the boundaries between climate and biotic interactions as determinants of regional and local dynamics respectively are largely artificial. Within local communities, climate has a strong influence on species interactions, resulting in complex community responses. Theoretical and experimental work has shown that increasing environmental temperature modifies population growth rate, carrying capacities, metabolic and ingestion rates [43], [44]. Also, warming alters universal properties of food webs, shifting body mass-abundance scaling relationships [45], and altering degree distributions by increasing diet specialization [46]. Similarly, climatic changes can alter the prevalence of top-down *versus* bottom-up control in aquatic ecosystems [47] and can affect profoundly several ecosystem processes, including productivity, ecosystem respiration and decomposition rates [45], [48], [49]. All taken together suggest that modifications of large-scale processes, such as climate, have profound consequences in local communities, mostly mediated by species interactions.

Less clear is the relevance of biotic interactions at large spatial extents. In a recent review, Wisz and colleagues [36] showed compelling evidence on the effects of biotic interactions determining the current (and past) distribution of species across multiple taxa and habitats, including competition, facilitation, herbivory and predation. Similarly, species new ranges that result from climate change are highly dependent on their interactions with other species [50].

Let's reconsider the latitudinal diversity gradient. Most hypotheses suggest that abiotic factors are responsible for finding species richness peaking in equatorial regions and declining towards the poles. Among these factors, the water-energy tandem, and historical climatic stability have received strong support across taxa and continents [29], [30]. The role of biotic interactions hangs in any discussion about the gradient. Yet its relative importance against abiotic factors is difficult to test because the quality and resolution of biotic interaction data across large spatial scales is very low in comparison to the quality and resolution of most abiotic drivers. However, its conceptual and theoretical basis are firmly established. Dobzhanski [51] proposed that the benign, constant climate in the tropics led to a greater importance of biotic interactions, resulting in tropical species more specialized and tropical communities harbouring greater species diversity. In contrast, the severe and variable climate in temperate regions resulted in the evolution of a few generalized species. Schemske and collaborators [37], [52] formalized this, and they suggested that more intense biotic interactions in the tropics promoted coevolution resulting in faster adaptation and speciation (Figure 5). New species introduce new resources and interactions, hence expanding the number of niches and creating a positive feedback of diversity. Similarly, resource specialization has been suggested as one explanation for the observed latitudinal gradient in species

richness: specialization reduces interspecific competition and facilitates species coexistence by partitioning niche space ([31]–[33] but see [34]).

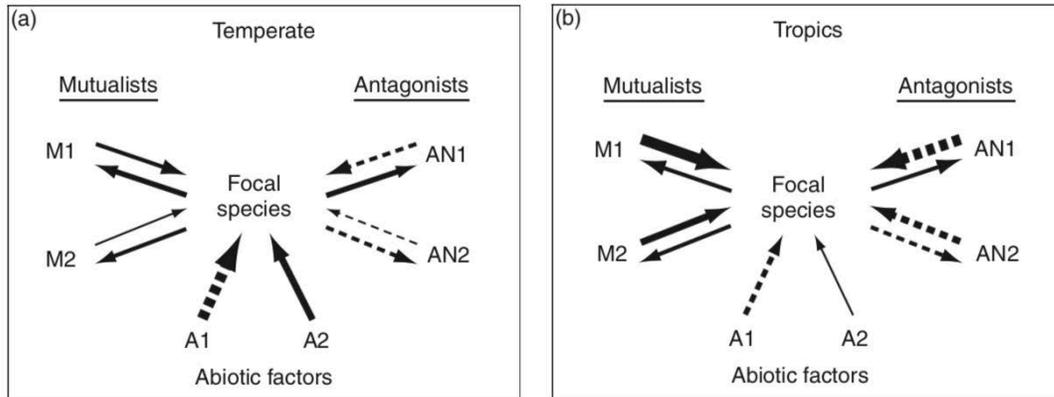


Figure 5. Interaction strengths in temperate and tropical communities. Arrows indicate the proportion of variation in fitness for a given focal species caused by biotic interactions with mutualists or antagonists, or by different abiotic factors. Positive interactions are represented by solid lines and negative interactions by dashed lines. Redrawn from [37].

The temporal scale under consideration also differs between network and biogeographical approaches, somehow echoing processes operating at different spatial scales. Although in both cases present day species composition, abundances and distributions are the focus, the hypothesized determinants typically operate over short-term, i.e., ecological time-scales, in network studies, while they operate over long-term, i.e., evolutionary and geological time-scales, in biogeographical research. There are only a few network studies that consider an evolutionary dimension, allowing for speciation dynamics (e.g., [53], [54]) or coevolution (e.g., [55]), although there is a recent interest in assessing the interplay between ecological and evolutionary dynamics, i.e., eco-evolutionary dynamics, in species interaction networks [56], [57]. In addition, a recent study showed the influence of historical climate change on the modularity and nestedness of pollination networks [58], suggesting that climatic stability over evolutionary time-scales was at least as important as current climate to understand present day networks. In contrast, geological and past evolutionary changes are widely used for explaining biogeographical patterns. Time-for-speciation, for example, is one of the central determinants of the latitudinal diversity gradient for a broad variety of plants and animals, by which past climatic stability in the tropics as opposed to glaciation cycles in northern hemisphere temperate areas could explain the pattern [59], [60].

Exceptions found at the interplay: Biogeographical changes in network structure

Kitching pioneered the study of biogeographical gradients of food web structure. Using the communities associated to *Phytotelmata* (i.e., water bodies in terrestrial plants) he showed that several food web properties varied across a latitudinal gradient. In particular, increasing latitude decreased mean food chain length and predator generalism [61] - a measure of diet specialization. However, Kitching's studies had small sample sizes and relatively simple food webs. Interestingly though, both food chain length and diet specialization have received attention in more detailed and comprehensive studies along environmental gradients.

Several hypotheses try to explain the observed variation in food chain length across habitats (see [62] for a review). Some hypothesized processes vary along geographical gradients. That is the case of resource availability: the more productive the system, the longer the food chains and/or the trophic position of the top predator. However, resource availability has limited predictive power, limiting food chain length only in systems with very low resource availability. Ecosystem size (area or volume) appears as the best predictor of food chain length [28], although the components of ecosystem size (e.g., habitat availability and heterogeneity, species diversity) that explain the pattern are not clear yet. Thus, variation in food chain length seems to be determined by a combination of local factors and large-scale processes.

Diet specialization is at the core of research in both ecological networks and biogeography. The general perception among ecologists is that biotic specialization increases towards the tropics. More generally, environmental constancy (or stability) leads to higher specialism. Community ecology and biogeography seem to agree historically in this respect. MacArthur [63] stated that the greater stability and lower seasonality in the tropics lead populations at low latitudes to be more stable than populations at higher latitudes, and, in turn, greater population stability should allow for narrower (and more specialized) diet niches. It has been shown that both past and contemporary climate stability influence biotic specialization [64]. The former reflecting the available time for species coevolution due to temporal stability of local communities [65] and contemporary climate determining the relative abundances and densities of resource species (by means of species diversity) which, in turn, regulates consumer species searching times [66], [67]. Longer search times constrain the specialization of consumer species [68] and therefore, warm climates (i.e., tropical regions with higher diversity of resource species) are supposed to lead to higher specialization of biotic interactions.

Recent studies have characterized latitudinal patterns in biotic specialization, showing non-conclusive and highly idiosyncratic results [69]. While some authors showed an increase in network specialization towards the tropics [70]–[72], others found the opposite [64]. Yet some others found distinct trends for each hemisphere [73] and for each measure of biotic specialization considered [74], or no latitudinal trend at all [75], [76].



Figure 6. Latitudinal patterns of specialization for frugivorous birds and their fruit plants. Dalsgaard and colleagues [74], found an opposed latitudinal pattern of network-derived and assemblage-level dietary specialization. That is, tropical communities mainly consist of obligate frugivorous birds, which form generalized interaction networks, while high latitude communities consist of bird species with an omnivorous diet containing both fruits and a wide range of other food types, but form specialized networks of interactions with their fruit plants. In the network, birds are at the left and plants at the right; link thickness reflects the pairwise frequency of interaction, and bar size illustrates the total number of interactions for each species. Redrawn from [74].

This high disparity of results arises partially because most large-scale studies on ecological networks are based on a significant variety of methods and protocols [77], including the use of different spatial scales to define a local community which, as will be explained in the following sections, can have important effects on the structure of ecological networks and therefore, can influence the comparisons between studies. In a recent study, Roslin and colleagues [78] assessed the latitudinal gradient in biotic interaction strength using a global experiment and they found that predation risk increased towards the equator (i.e., higher biotic interaction strengths), with a parallel pattern of increasing predation towards

lower elevations (Figure 7). Interestingly, they found similar gradients across spatial scales (i.e., at global and regional scales), suggesting that the mechanisms underlying biotic interaction strength might be consistent across spatial scales.

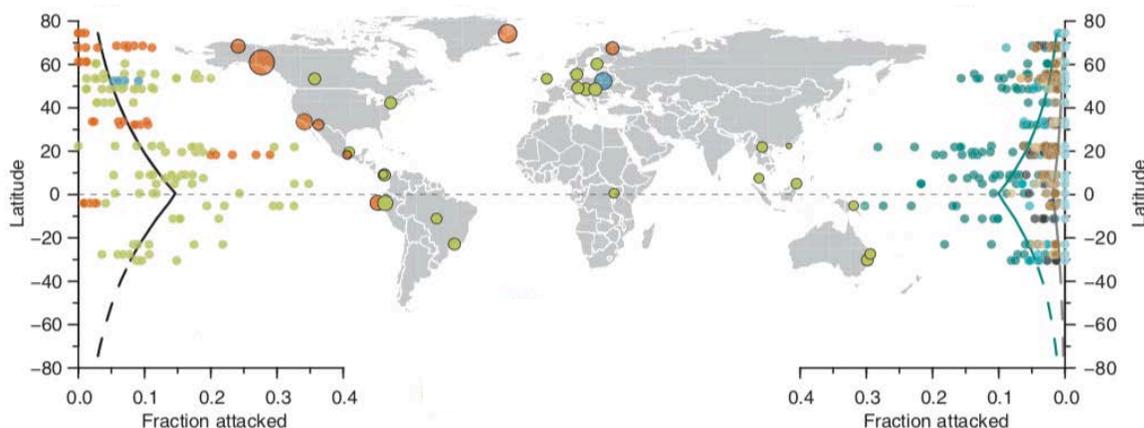


Figure 7. Map of sampling sites with scatter plots showing fates of model caterpillars at different latitudes. In the map, individual sites are shown with symbol size graduated by the individual exposure. The panels show the overall fraction of caterpillar models attacked per day (i.e., daily predation rates per model caterpillar) coloured by habitat type (left panel) and by predator type (right panel).

The emergence of such studies bridging the gap between ecological network research and biogeography shows that the cross-disciplinary boundaries are largely artificial, and that much progress can be made through the adoption of both a biogeographical perspective in networks and a network perspective in biogeography. Further analyses are needed to progress towards the complete understanding of biogeographical patterns in network structure, contemplating both present-day and historical determinants. In the first chapter of the thesis, I explore the geographical gradient of different facets of network specialization, putting special attention on the influence of the spatial scale of observation which, as explained in the following section, is at the bases of other efforts integrating large-scale processes into species interaction networks.

THE SPATIAL SCALING OF ECOLOGICAL COMMUNITIES

The spatial scaling of biodiversity: beyond Species-Area Relationships

Research on the spatial scaling of biodiversity has traditionally focused on the increase in species richness with area size [79]–[81]; so much so that the species-area relationship (SAR) has been identified as a universal law in ecology [81]–[83]. MacArthur and Wilson (1967) proposed in their *Theory of Island Biogeography (TIB)* the diversity-dependent dynamic balance between immigration and extinction as a determinant of island species richness. In their model, species immigration rate for an island decreases as the number of species on the island increases and species extinction rate increases with the number of species, implying that diversity will reach the equilibrium. The *TIB* assumes that the closer the island is to the mainland the larger the colonisation rate [80], and that the larger the island size the lower the extinction rate due to the increase in population sizes [84], [85], resulting in a positive relationship between species richness and area size (Figure 8).

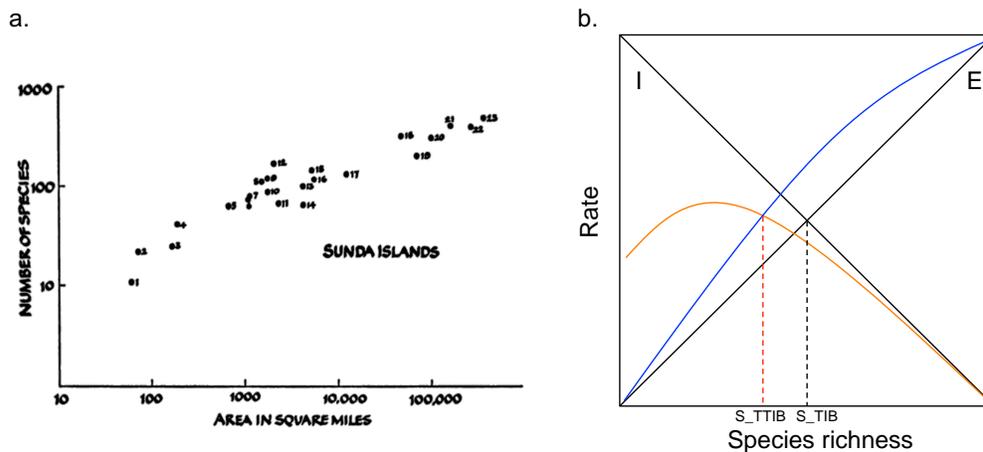


Figure 8. Theory of island biogeography adapted from [80] and its trophic extension from [86]. In (a) the number of land and fresh-water bird species on various islands of different area sizes of the Sunda archipelago, together with the Philippines and New Guinea. In (b) the classic TIB depicted in black. Equilibrium species richness (S_{TIB}) is reached when immigration rate is equal to extinction rate (intersection between I and E; i.e., black dotted line). TTIB is depicted in colors (orange and blue for immigration and extinction rates, respectively). Equilibrium species richness (S_{TTIB}) is represented by the red dotted line.

Even though MacArthur and Wilson already stated that the “interference” between species might shape the extinction curve, they did not address explicitly the effect of considering interspecific interactions. Following early efforts by Holt [87], [88], Gravel and colleagues [86] extended the classic island biogeography theory to account for trophic interactions assuming bottom-up trophic dependencies: a species needs the presence of at least one of its prey items to establish and persist in an island. Given that colonization by higher trophic levels cannot occur until the lower ones have established, the trophic theory of island biogeography (TTIB) predicts a slower accumulation of species affecting the classic equilibrium point (Figure 8). Thus, TTIB shows that considering a trophic constraint on species immigration and extinction would affect the richness of the local assemblage and their biotic interactions, where species that are diet generalists and/or belong to lower trophic levels are preferentially selected given that they are less affected by the trophic constraint.

The interplay between local and regional processes was already established in the study of local diversity [89]–[91]. Regional processes operating at large spatial scales, such as species dispersal from a regional propagule supply, are important determinants of local diversity in both terrestrial and marine systems [92]. However, this new community perspective on the classical theory of island biogeography [86]–[88], [93], shows how large-scale processes can influence not only the species richness of the local community but also its composition and structure, opening new avenues for the interaction between biogeography, networks and spatial dynamics.

Multi-trophic SARs and Network-Area Relationship

For several logistic reasons, most studies of species-area relationships have been traditionally limited to particular taxa and functional groups [94]. SARs for multi-trophic communities are just starting to be documented [95]–[97], along with the role played by biotic interactions in shaping these relationships [96], [98]. Yet, ecological communities are not only collections of species, but also sets of interactions between them. Therefore, if we aim to understand how ecological communities change across spatial scales, and how they will respond to perturbations such as habitat loss or fragmentation, we also need to determine how biotic interactions and the emerging network structure of multispecies communities change according to the location and size of the area sampled (Figure 9).

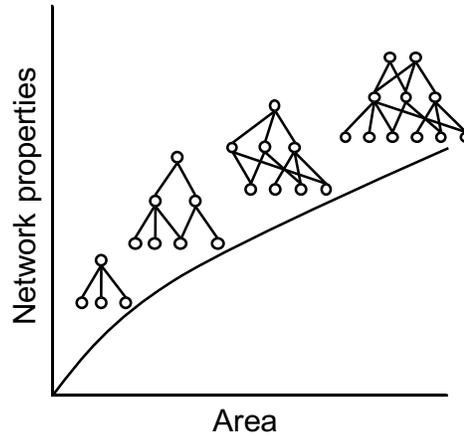


Figure 9. Network-Area Relationships (NARs). The spatial scaling of biodiversity should be measured in terms of both species and their biotic interactions. The species-area relationship is one of the most well-known patterns in ecology, which has been extensively used to estimate species richness in a given region and to predict species extinctions due to habitat loss. To fully understand the response of ecological communities to perturbations we need to extend the knowledge we have on SARs to the entire community and start exploring NARs.

It is well established that species richness affects several food web properties. In many cases, differences in network properties might be strongly related to the differences in species richness between the communities studied [99]–[103]. For instance, there is a well-studied relationship between species richness and the number of interactions present in ecological networks. Two major hypotheses have been proposed to explain the variation in the number of links with species richness. While the ‘link-species scaling law’ [104] states that species interact with a constant number of species independently of species richness [105], [106], the ‘constant connectance hypothesis’ [107] states that what is constant is the connectance of the network (i.e., the fraction of potential interactions that are realized), irrespective of species richness. Empirically, it has been shown that link-species relationships lay in between the two [8], [108]. Both hypotheses do not explicitly account for the effect of area size on species richness. Brose and colleagues [109], proposed a scaling of trophic links with area by combining the species-area relationship with the link–species relationship. Given that species richness increases with area, and the number of links scales with species richness, changes in food web structure with area are expected to emerge simply from SAR, which are in turn shaped by the specific link-species relationship in place.

However, other processes can underlie changes in network structure across spatial scales independently of species richness. For instance, Roslin and colleagues [96], recently showed that the slope of SARs steepens from plants to herbivores and from primary to secondary parasitoids, triggering a decrease in food chain length from large to small islands. If the spatial scaling of species richness differs among trophic levels, different facets of network structure are expected to change with area [88], [95], [96]. Similarly, Pillai and colleagues [110] used a meta-community model to explain how network complexity can increase as the spatial extent increases when omnivorous and generalist species connect local patches (Figure 10).

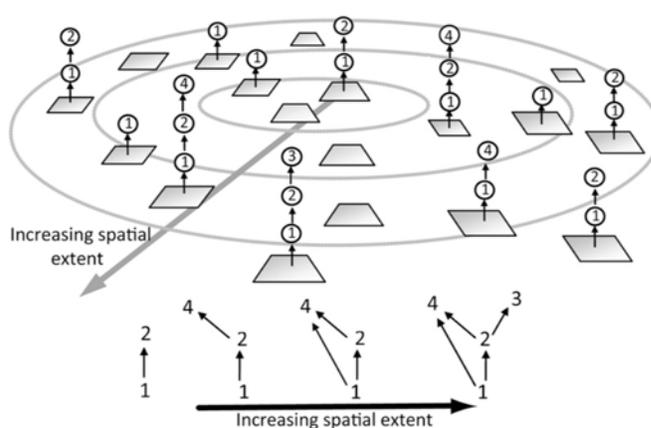


Figure 10. Example of how food web complexity might emerge at large spatial scales through the spatial aggregation of local food chain networks with increasing spatial extent within a meta-community. As spatial scale increases, and as more species and potential feeding interactions are sampled, the observed trophic complexity of the regionally aggregated food web. Figure taken from [110].

Gaining a deeper understanding of network-area relationships (NARs) is arguably as important as the knowledge we have on SARs. Indeed, understanding the mechanistic basis of the spatial scaling of network properties is not only crucial to better predict the effects of habitat disturbances on the organisation of multispecies communities, ultimately affecting their persistence and functioning, but also to be able to interpret empirical data on ecological networks. If the spatial scale affects network structure, then comparative studies should explicitly consider the area sampled to generate meaningful conclusions, as it is systematically done on studies on diversity distribution patterns [111]. In the three last chapters of the thesis, I explore the mechanisms behind the changes in network structure across spatial scales, and which are the environmental factors affecting the shape of the spatial scaling observed.

New methods and tools for macroecological networks

Moving into macroecological networks requires new methods and tools to approach them. Empirically documenting network structure at large spatial scales, can be extremely costly and time-consuming [112]. Especially if one attempts to analyse vast ranges of spatial extents, like it has been done for SARs. The use of potential networks of biotic interactions, or 'metawebs' (*sensu* [5]), provides an alternative approach to analyse ecological networks at these large spatial scales (Figure 11). The structure of such potential networks can be based on pure random interactions between the overall regional pool of species, or can further account for the species distribution [113], trait matching [112], [114], [115], or phylogenetic relatedness [116]. Thus, instead of assembling each local ecological network solely relying on observed interactions, one can infer the local occurrence of biotic interactions between all the species in the regional pool based on expert knowledge on who eats whom, species traits or phylogenies, coupled with measurable information on species distributions and environmental conditions.

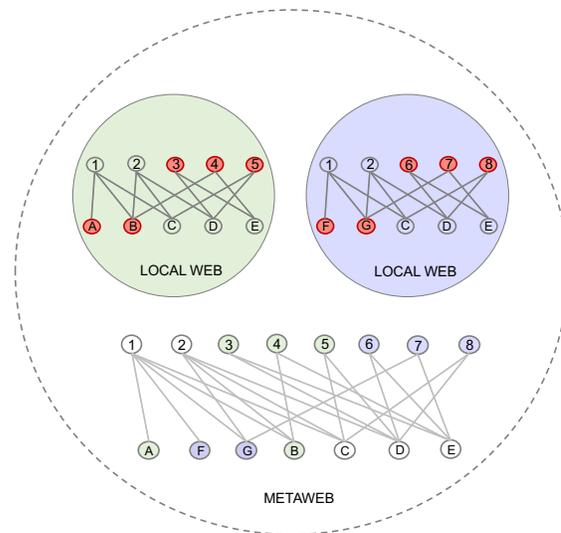


Figure 11. Conceptual representation of a metaweb. Circles coloured in green and purple represent two local assemblages with consumers represented by the numbered nodes and resources by the nodes with letters. Lines connecting nodes represent biotic interactions (i.e., links). Nodes in red represent those species that are not present in both local communities. The metaweb, represented at the bottom of the figure, combines both local communities including all species present in both local webs and their biotic interactions. The links depicted in the local webs can be observed or inferred based on different constraints described in the text, such as species co-occurrence in space.

The comparison between the local assemblages with the metaweb can inform not only on whether the latter provides a good approximation of the realised networks but also it can provide valuable information on the processes that structure communities at different spatial scales and along large-scale environmental gradients. For example, if some local structure deviates more than others in particular parts of the environmental gradient, it might reflect higher levels of beta-diversity that generate more variation in species composition and in their biotic interactions across space and, in turn, larger changes as we scale up in space.

Similarly, Kissling and coauthors [117] suggested novel approaches to incorporate biotic interactions into species distribution models (SDMs), which had traditionally ignored the role of species interactions. They proposed the use of multispecies co-occurrence datasets across large-scale environmental gradients to infer potential interaction matrices, coupled with comprehensive spatio-temporal data on biotic interactions to incorporate the non-stationarity in interaction coefficients across space and time. Although challenged by the limited empirical knowledge on the spatio-temporal variation of species interactions, they highlighted the great potential for developing novel approaches that incorporate multispecies interactions into the projection of species distributions and community structure at large spatial extents. Therefore, the use of all the new emerging tools to assemble ecological communities, together with increasingly powerful predictive models for species distributions, is not only necessary to analyse and quantify network structure at large biogeographical scales, but it also opens new avenues to further understand ecological communities and the processes structuring them.

SUMMARY OF THE CHAPTERS

The general objective of this thesis is to incorporate spatial and biogeographical processes into ecological network research to develop a more holistic understanding of ecological systems across spatial scales. To do so, the thesis is organized in 4 chapters, each addressing different aspects of the interaction between ecological networks, biogeography and spatial processes (Figure 12). I use an integrative approach that combines theory and data analyses to investigate different facets of this interaction in order to build a comprehensive view on macroecological networks. In this section I briefly summarize each chapter describing their motivation, objective and questions posed, methodology used and the main findings and conclusions.

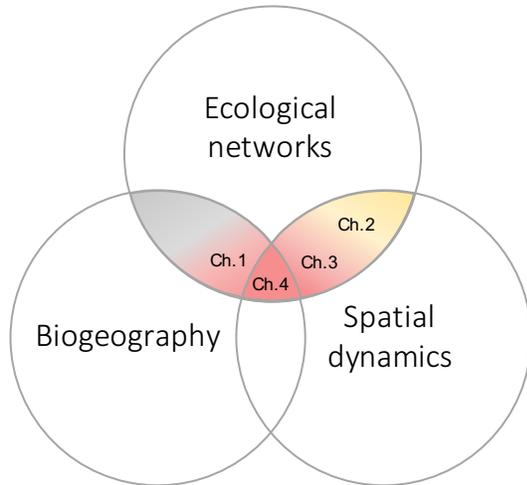


Figure 12. Conceptual representation of the thesis. Each chapter represents a different level of the integration between ecological networks, biogeography and spatial dynamics. Chapter 1 integrates ecological networks and biogeography, focusing on the effect of the spatial scale of observation. Chapter 2 and 3 analyse the spatial scaling of network structure incorporating some biogeographical concepts and mechanisms. Chapter 4 integrates all fields by analysing the geographical variation of the spatial scaling of network structure.

Chapter 1: Geographical variation of network structure

Motivation. The latitudinal variation in biotic specialization has long interested ecologists. Biotic specialization has historically been thought to be higher in more constant environments like the tropics. Yet, recent studies have challenged this view by showing non-conclusive and highly idiosyncratic results. However, all studies have analysed biotic specialization at the local scale, ignoring how specialization at larger spatial extents varies along the same biogeographical gradient.

Objectives and questions. The first chapter of the thesis aims to analyse **how network structure changes across large biogeographical gradients of environmental constancy**. Specifically, I use a global dataset of 173 host (resource)-parasitoid (consumer) networks to investigate (1) whether different facets of network specialization exhibit a pattern along the biogeographical gradients of both current and historical climatic constancy and (2) whether these patterns are scale-dependent, i.e., whether the patterns observed in local networks are different from those observed in networks described at larger spatial scales.

Main results and conclusions. I show that **the geographical gradient of biotic specialization is not universal. It depends on both the facet of biotic specialization analysed and the spatial scale of observation.** While networks at the regional scale did not show a geographical variation, at the local scale, network connectance, consumer diet overlap and resource vulnerability increased along the gradient of environmental constancy whereas consumer generalism decreased (i.e., broader diet breadths in tropical areas).

Chapters 2 and 3: Effects of area size on network structure- Theory and Data

Motivation. The spatial scaling of biodiversity has been traditionally understood as the spatial scaling of species richness. Yet, species are embedded in complex networks of biotic interactions and whether different components of network structure vary with area size is, so far, unknown. Exploring the importance of area size for community structure can help to extend the knowledge we have on the effects of habitat loss and fragmentation on ecological communities in a changing world.

Objectives and questions. The second and third chapters of the thesis are thus devoted to **understanding the spatial scaling of network structure**. That is, how different aspects of network structure change across spatial scales. Specifically, in Chapter 2 I use several theoretical models to explore the underlying mechanisms giving rise to changes in network structure as areas become larger. In Chapter 3, I explore the empirical evidence of these spatial scalings. I investigate the universalities in the spatial scaling of network structure and tests the theoretical predictions developed in Chapter 2 using 35 data sets of ecological networks from different ecosystems and biomes across the globe, that comprise different types of interactions (i.e., mutualistic, antagonistic) and different sampling methodologies.

Main results and conclusions. In Chapter 2, I develop a new theoretical framework that allowed me to present a number of Network-Area Relationships (NARs) for multi-trophic communities emerging from different spatial processes. Mainly, **network structure changes as area increases because of the existence of different Species-Area relationships (SARs) across trophic levels, the preferential selection of generalist species at small spatial extents, and the effect of dispersal limitation promoting beta-diversity**. This theoretical approach constitutes the foundations to understand the mechanisms behind the structure of ecological communities across spatial scales.

In Chapter 3, I found **a number of universal NARs**. Namely, the number of links, links per species and mean indegree (i.e., mean number of resources per consumer) increase with area size following a power law regardless of the data category or interaction type. This suggests that ecological **communities become more complex with area**. In contrast, mean potential indegree (i.e., mean number of resources a consumer has at the regional scale) decrease across spatial scales, suggesting that **specialist species require larger areas to be found**.

Chapter 4: Geographical variation of the spatial scaling of network structure

Motivation. Understanding the factors that determine the shape of SARs is at the heart of ecology and biogeography. Several factors have been proposed to explain the variation found in the strength and slope of SARs. To progress towards a more comprehensive understanding of the determinants of the spatial scaling of ecological communities, we need to explore which factors affect the shape of NARs.

Objectives and questions. The fourth chapter of the thesis aims at integrating the three components of the thesis (i.e., ecological networks, spatial processes and biogeography) by analysing the spatial scaling of network structure across different biogeographical regions in Europe. The main objective is to determine whether there is **geographical variation in the specific shape of NARs**, what are the main **environmental determinants of the variation** observed between biogeographical regions and what is the **contribution of species richness** for the patterns observed. To do so, I use a subset of the data used in chapter 3 to constrain the sources of variability to only environmental factors. Specifically, I analyse how network structure changes with area size in Europe using the biogeographical regions that it comprises as independent samples to understand the effects of different environmental factors on the shape of NARs.

Main results and conclusions. I find that **the spatial scaling of network complexity strongly varies across biogeographical regions. However, once the variation in the spatial scaling of species richness across Europe is accounted for, differences in the shape of the NARs disappear.** Instead, network vertical diversity properties, such as the **proportion of species per trophic level, remain remarkably stable** across biogeographical regions and across spatial scales. The spatial variation in the mean annual temperature and the spatial clustering of habitats show to be the main determinants of the spatial scaling of ecological communities across Europe.

Chapter 1

GEOGRAPHICAL VARIATION OF NETWORK STRUCTURE

1.1 TITLE OF THE SCIENTIFIC ARTICLE:

The geographical variability of network structure is scale dependent²

Keywords: consumer-resource, host-parasitoid foodwebs, environmental constancy, geographical scale, spatial scale, network structure, biotic specialization, biogeographical gradients, beta-diversity.

ABSTRACT

Research on the structure of ecological networks suggests that a number of universal patterns exist. Prevailing wisdom states that biotic specialization increases towards the Equator. However, recent studies have challenged this view showing non-conclusive results. A major limitation of the studies analysing the geographical variation in biotic specialization, is their focus on the local scale. Little is known about how the spatial scale of observation (i.e., from local to regional spatial scales) affects the geographical variation of network structure. This should be remedied, as network structure changes as the spatial scale of observation changes, and the magnitude and shape of these changes can elucidate the mechanisms behind the geographical variation in biotic specialization. Here we analyse four facets of biotic specialization in host-parasitoid networks along gradients of climatic constancy, classifying the networks according to their spatial extension (local or regional). While at the regional scale climatic constancy is not a good predictor of biotic specialization, at the local scale network connectance, consumer diet overlap and resource vulnerability increased along the gradient of environmental constancy whereas consumer generalism decreased (i.e., broader diet breadths in tropical areas). We provide an explanation based on different beta-diversity for consumers and resources across the geographical gradient. Our results show that the geographical gradient of biotic specialization is not universal. It depends on both the facet of biotic specialization and the spatial scale of observation.

² This article represents a collaboration with Bradford H. Hawkins and José M. Montoya. It is in 2nd review in *Ecography*.

1.2 INTRODUCTION

Large networks of species interactions display a number of universal patterns across habitats and interaction types, which likely determine the response of ecosystems to environmental changes [4], [6]–[10]. However, research on ecological networks has challenged some patterns emerging from the study of simple pairwise and isolated interactions. Reciprocal specialization, for example, that occurs when a consumer specializes on a resource and vice versa, is rare when the whole network of interactions is considered [118].

Prevailing wisdom states that biotic specialization is higher in more constant environments. Hypotheses for this pattern include the supposition that greater stability and lower seasonality in e.g. the tropics, lead to more stable population dynamics than those at higher latitudes, allowing for narrower (and more specialized) feeding niches [63], [119]. Similarly, more historically constant environments reflect the available time for potential species coevolution due to temporal stability of local communities, which increases local adaptation and favours biotic specialization [58], [64], [65], [71]. Recent studies have addressed the geographical variation in biotic specialization, showing non-conclusive and highly idiosyncratic results [69]. While some authors showed an increase in network specialization and higher predation risk towards the tropics [70]–[72], [78], others found the opposite [64]. Yet some others found distinct trends for each hemisphere [73] and for each measure of biotic specialization considered [74], or no latitudinal trend at all [75], [76].

All studies to date focused on specialization across local communities, ignoring how specialization at larger spatial extents (e.g., regional scale) varies along the same biogeographical gradient. This is crucial, as several spatial processes largely affect food web structure and dynamics [86], [87], [120]–[122], fostering changes in network structure as the spatial scale of observation changes [96], [103], [110], [123], [124]. For instance, given that not all species react similarly to landscape configuration [125], we can observe differences in the slopes of the species-area relationships (SAR) across trophic levels that, in turn, can generate further changes in network structure across spatial scales [88], [95], [96], [124]. These differences in the slope of SARs across trophic levels can reflect differences in β -diversity (i.e., site-to-site variation in community composition) across trophic levels, when the total extent of area and the size of the regional pool of species are accounted for [126], [127]. If β -diversity is different across trophic levels [128], and therefore there is an unbalanced increase in the number of species per trophic level as area size increases, the structure of the network will change across spatial scales. For example, if consumers' β -diversity is higher than resources' β -diversity, the number of species consuming a resource might

increase from local to regional spatial scales due to the larger increase of consumer species than resource species. In addition, if the differences in beta-diversity across trophic levels are not universal, changes in network structure across spatial scales might vary geographically. Indeed, β -diversity provides a direct link between biodiversity at local scale (α -diversity) and the broader regional pool of species (γ -diversity) [129], [130]. This connection allows for a better understanding of the processes that structure communities at different spatial scales and that can, in turn, be the basis of the geographical gradients of biodiversity [131]–[133].

Moreover, interactions among species can differ among environments, experiencing spatial turnover independent from species occurrences [134], [135]. The realization of an interaction between two species that co-occur in space is directly influenced by the surrounding environment and how this affects each species [134], [136], [137]. Therefore, scaling up in space allows to capture the potential network of interactions and the potential mechanisms behind the variation of network structure in space or along large environmental gradients. Indeed, a regional network (or metaweb) characterizes all potential interactions among all species that are susceptible to both co-occur and interact at the scale considered [5], [112], [115]. The motivation for comparing local and regional networks is thus similar to the implicit motivation for comparing local and regional diversity: what and how spatial processes affect the changes of network properties or richness.

Here we focus on how the spatial scale of observation (i.e., local vs. regional) affects the geographical gradient of biotic specialization. The idea that the degree of specialization increases towards the Tropics has been rarely explored beyond niches becoming narrower, that is, beyond specialization from the consumers' perspective [34], [63], [119]. However, specialization is a multifaceted concept; there are other dimensions of biotic specialization beyond diet breadth, such as network-based metrics that reflect the general level of specialization of the community [74], [138], [139]. This is important since different facets of specialization can reveal different patterns across environmental gradients [74]. Here we analyse four facets of biotic specialization: network connectance, consumer diet overlap, consumer diet breadth (or generality), and resource vulnerability at both local and regional spatial scales along two environmental gradients. Namely, current climatic constancy (i.e., annual temperature range) and historical climatic constancy (i.e., the change in mean annual temperature at a given location since the Last Glacial Maximum, 21.000 years ago to present). We also analyse the number of species at each trophic level at both spatial scales to determine the possible contribution of β -diversity to the spatial scaling of network structure along the environmental gradient. We expect changes in network structure

across spatial scales to emerge due to unbalanced increases of species richness per trophic level as the spatial scale of observation changes. Following the biotic specialization hypothesis, we would expect networks to be more specialized in more constant climates, both historically and contemporaneously. That is, less connected networks, with consumer diets being more specialized and less overlapped and resources being attacked by fewer consumers.

We use a global dataset of 173 host (resource)-parasitoid (consumer) networks (Figure 13) to investigate (1) whether different facets of network specialization exhibit a pattern along the biogeographical gradients of both current and historical climatic constancy and (2) whether these patterns are scale-dependent, i.e., whether the patterns observed in local food webs are different from those observed in regional food webs.

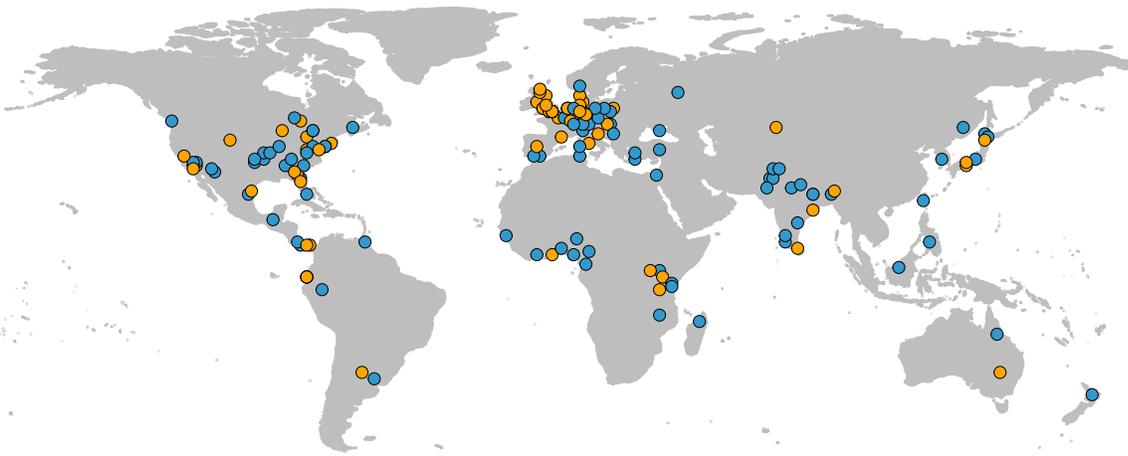


Figure 13. Localization of the 173 host (resources)-parasitoid (consumers) bipartite networks analysed. Each point corresponds to a network, with orange and blue for local and regional respectively.

1.3 METHODS

1.3.1 Data set

We compiled and analysed 173 host (resource)-parasitoid (consumer) bipartite networks occurring in a globally extensive range of habitat types extracted from a parasitoid assemblage diversity database initiated by Hawkins (1990, 2005) and extended into the present (Figure 13). In these networks, species correspond to taxonomic species (i.e., we avoid aggregation into trophic species), and links always correspond to direct observations of a larval parasitoid insect feeding and developing within or on its herbivorous insect host. Only webs composed of more than 10 species (hosts and parasitoids altogether) were considered, with a minimum of 2 species within each trophic level. We only considered binary data (i.e., the presence or absence of an interaction) given that data on interaction strengths for regional food webs were not available.

Most data on the structure and strength of ecological interactions are snapshots in time and space [140]. However, both feeding links and interaction strengths vary over time and space as a function of abiotic conditions, population densities, predator switching or due to non-linear functional responses [24], [141]–[144]. All these factors make the averaging of interaction strengths across local communities to obtain the interaction strength at the regional scale both problematic and unrealistic. More sophisticated studies that directly measure interaction strength accounting for these variations in population densities and functional responses across spatial scales are needed to obtain this information.

1.3.2 Environmental variables

We focused our analyses on the effect of temperature variability, both contemporary and historical, on network structure. For that, we used annual range in temperature and historical-climate change as predictor variables respectively. The annual temperature range of the location of each network was extracted from the worldclim database [145], corresponding to *bio7* (Max Temperature of Warmest Month - Min Temperature of Coldest Month). Although traditionally the geographical gradient of biotic specialization has been tested using latitude as the predictor variable, here we used temperature range because it provides more direct measures of local climatic conditions and allows us to directly test the effect of climatic constancy on biotic specialization [146]. Historical climate-change was calculated using the mean annual temperature 21.000 ybp, provided by the tool *PaleoView* [147], and the mean annual temperature from worldclim (i.e. difference between current mean annual temperature and mean annual temperature 21.000ybp).

1.3.3 Spatial scale: local versus regional networks

To test the influence of the spatial scale on food web structure, we distinguished between local and regional food webs. The spatial scale of each network was determined based on the area covered during the data collection of each study described in each publication analysed. In all cases, we considered the original network described in each publication and the spatial scale addressed originally, i.e., we did not build any network, neither local nor regional, from the aggregation of other published local webs or inferred interactions between species. Local webs are those collected from a single sampling site or from multiple sampling sites covering an area smaller than 1000 km². Regional webs are those collected from multiple sampling locations distant from each other covering areas larger than 1000 km². Therefore, while local networks represent the realised interactions between species of the local assemblage, regional networks represent the combination of all the interactions between species that have been observed in at least one of the locations sampled within the scale considered, which does not entail that they are necessarily realized in every single location within the area covered by the regional network. Thus, regional networks represent all potential interactions among species from the regional pool that are susceptible to both co-occur and interact at the scale considered [5], [112], [115]. We considered the threshold commonly used in the literature for local versus regional species diversity [39], [148] to also determine local and regional spatial scales for biotic interactions. We considered spatial scale as a categorical variable because accurate estimations of the area sampled were not available in all publications, which makes them not reliable enough across a continuum. We tested the robustness of our results by varying the threshold used from 500km² to 1000km² and it did not affect the results.

1.3.4 Network properties

In our bipartite host-parasitoid networks, species richness (S) is the sum of the number of species of resources (S_R) and consumers (S_C). We measured structural properties of food webs that correspond to four facets of network specialization:

- *Connectance* (C) is the number of actual links (L) divided by the number of possible links in the bipartite network ($S_R * S_C$).
- *Consumer diet overlap* (O), is the connectance of the consumer overlap graph, where a link between two consumers exists if they share, at least, one resource species (Cohen 1978, Sugihara 1984). Consumer overlap is thus the actual number of links among consumers (L_C) divided by the possible links between them ($S_C * (S_C - 1) / 2$). This property describes the extent and pattern of resource-use overlap amongst consumers and indicates the potential for indirect (that is, exploitative) competition [106].

- *Diet breadth or generality* is the mean number of resources per consumer species, that is, L/S_C . It is a measure of the degree of specialization in the web from the consumer perspective.

- *Vulnerability* is the mean number of consumers per resource species, L/S_R , and represents the degree of specialization found in the network from the resource perspective.

Additionally, we measured the number of species at each trophic level (i.e. number of parasitoids and hosts) and consumer:resource ratios. We analysed all these network properties at each spatial scale along the gradient of environmental constancy.

1.3.5 Control by species richness

Some of these structural properties can be sensitive to differences in species richness (S) among food webs [99], [103], [149], [150]. Therefore, comparative analyses of food webs need to control for variation in species richness across webs given that conclusions on the variability of food web structure might simply result from variation in species richness across webs [99], [103], [149], [150]. Controlling for S is particularly relevant in biogeographical studies, because a latitudinal gradient in species richness generally exists: S increases towards the tropics in most taxa [151], [152]. We thus controlled all the analyses for species richness S ($S = S_R + S_C$) including it as a covariate in our statistical analyses, and this should partially correct for different sampling efforts in the field among studies since observational effort and species richness correlate strongly [153], [154]. Due to the lack of quantitative data, further analyses to control for sampling effort were not possible. In addition, we also perform all the analyses controlling by the number of species in each trophic level independently (i.e., including them individually as covariates in the models).

1.3.6 Beta-diversity analyses

Species β -diversity influences the changes in species richness from local to regional spatial scales. If β -diversity differs across trophic levels, changes in species richness from local to regional spatial scales will be unbalanced, and the trophic level with higher β -diversity will experience a larger increase in species richness across spatial scales. This will lead to changes in network structure across spatial scales. We thus hypothesize that differences in β -diversity across trophic levels can generate changes in network structure across spatial scales. Given that our dataset is composed by independent local and regional networks (i.e., our local networks are not subsets of our regional networks) and the information of the different local sites used to construct the regional networks is not available in most of the original papers, we cannot directly test this hypothesis with the data. However, to theoretically understand how β -diversity

influences the increase in species richness from local to regional spatial scales and how it can generate changes in network structure across spatial scales, we built three identical random local networks. These networks have the same number of species and links, with species equally distributed across trophic levels, which results on a consumer:resource ratio equal to 1. Interactions between species were randomly assigned from a uniform distribution between 0 and 1, where network connectance determined the probability for a consumer-resource link. We then defined β -diversity as the percentage of species co-occurring within each trophic level across local webs, reflecting their spatial turnover [155]. This gives two values of β -diversity, one for each trophic level: β_{consumer} - and β_{resource} -diversity (Figure 14).

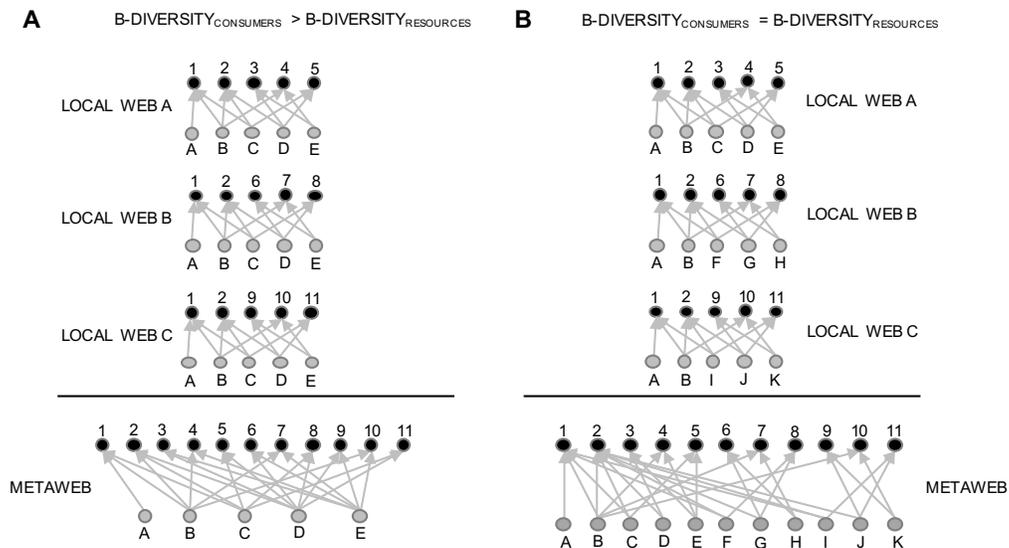


Figure 14. Beta-diversity as a mechanism for the variation on network structure across spatial scales. Black nodes represent consumer species and grey nodes resource species. Species identities are represented with numbers for consumers and letters for resources. Arrows correspond to species interactions. All local networks have the same number of species and identical structure. Properties of the local networks: connectance=0.48; consumer overlap=0.8; consumer diet breadth=2.4; resources vulnerability=2.4; consumer:resource ratio= 1. In (a) $\beta_{\text{consumers}}$ -diversity =0.6 and $\beta_{\text{resources}}$ -diversity =0. That is, 3 out of the 5 species of consumers are replaced in each local network while resource species have the same identity in the three local networks. The regional network (or metaweb) is built from the aggregation of the three local networks, where species maintain their identity and their interactions. Properties of the regional network (metaweb) in (a): connectance=0.43; consumer overlap=0.78; consumer diet breadth=2.18; resources vulnerability=4.8; consumer-resource ratio= 2.2. In (b) β -diversity =0.6 for both trophic levels. Properties of the regional network in (b): connectance=0.247; consumers' overlap=0.47; consumers' diet breadth=2.72; resources vulnerability=2.72; consumer-resource ratio= 1.

To determine the effect of having unbalanced values of spatial turnover (β -diversity) between trophic levels on the changes in network structure across spatial scales, we assigned values of β_{consumer} -diversity, ranging from 0.1 to 0.8 with an increase of 0.1, while we kept β_{resource} -diversity equal 0 (Figure 14a). On a different scenario, we varied simultaneously β -diversity across trophic levels. That is, we assigned values of β -diversity ranging from 0.1 to 0.8 with an increase of 0.1 to both trophic levels at the same time (Figure 14b). We then analysed network properties at both local and regional (i.e., the metaweb resulting from the aggregation of the three local networks) spatial scales.

1.3.7 Statistical analyses

We used GLMs (Family = Gaussian, Link = identity) to analyse differences in network properties depending on both environmental variables (dependent variables: network connectance, consumer overlap, consumer diet breadth, prey vulnerability, number of hosts and number of parasitoids; independent variables: annual temperature range and historical climate-change). Because our independent variables suffered from multicollinearity (adjusted- $R^2=0.38$), we could not perform a meaningful multiple regression analyses to partition the predictive power of the two environmental variables. Number of species was included into the GLMs as a covariate. Additionally, the number of hosts and parasitoids were also included individually as covariates except for the analyses where they were considered dependent variables. We performed the analyses with every network variable (dependent and covariate) and the environmental predictors log-transformed. Given that we expected the relationship of the dependent variables (i.e., network properties) and the environmental variables to be affected by the spatial scale of observation, we included spatial scale as an interaction term with the dependent variables in the statistical models. We used Type III sum of squares in our analyses due to our unbalanced data (local networks=74; regional networks=99). Following the statistical analysis, we confirmed that none of the network metrics contained significant spatial autocorrelation in the model residuals, (all $P>0.05$), which indicates that significance tests are unbiased.

1.4 RESULTS

1.4.1 Effects of environmental constancy on network structure

At the regional scale, network connectance, consumer diet overlap, consumer diet breadth, and resource vulnerability showed no significant changes along the gradients of annual temperature range and historical climate-change, except for a slight decrease of consumer diet breadth along the gradient of historical climate-change (Figure 15, Table 2). That is, the variation in network structure described at the

regional scale was not well predicted by the constancy of either current or historical temperature constancy.

On the contrary, for local webs, both environmental variables were good predictors of network structure. All network properties were significantly correlated with species richness at both spatial scales (Table S1.1, Figure S1.1). Even though there was no significant difference in the relationship of the number of species with the network properties across spatial scales (Table S1.1, Figure S1.1), the mean number of species was significantly smaller at local than at regional scales, as expected. We found no significant relation of species richness with neither of the gradients of environmental constancy (Table S1.2, Figure S1.2). Yet all results described in this section refer to the patterns observed after accounting statistically for the effect of the number of species. Additionally, we performed the analyses controlling by the number of species in each trophic level as two separate covariates and we obtained the same results for the gradient of annual temperature range while losing the trend for resource vulnerability at the local scale with the past climatic constancy gradient (Table S1.3).

Specifically, network connectance, consumer diet overlap and resource vulnerability increased along the gradient of annual temperature range, while consumer diet breadth decreased (Figure 15, Table 2). Therefore, local webs in more currently constant environments were less connected, their consumers overlapped less their diets and, in turn, prey vulnerability decreased, as expected from the biotic specialization hypothesis. However, consumer diet breadth (i.e., generality) showed the opposite pattern; it decreased in more climatic fluctuating environments. Historical climate-change predicted similar patterns for prey vulnerability and consumer diet breadth than annual temperature range. That is, the larger the change in climate over the last 21.000 years, the larger the number of predators attacking a given prey and the fewer the mean number of prey a predator has (Table 2, Figure 15). However, current climatic constancy was a better predictor of biotic specialization at the local scale than historical climatic constancy (cf. R^2 values and significances in Table 2 and Table S1.3). Therefore, local networks in more climatically constant environments, both historically and contemporaneously, show opposite results for resource and consumer species. From the resource perspective, local networks are more specialized (i.e., resources have lower vulnerability) in climatically constant environments but, from the consumer perspective, they are less specialized (i.e., consumers are more generalist) (Table 2, Figure 15).

Table 2. GLM results for the relationship of each network property with annual temperature range and past climate-change. Estimates, T values and statistical significances (***) for p-values<0.0001; ** for p-values<0.01; * for p-values<0.05; ° for p-values<0.1) are indicated for the relationship at each spatial scale - local (N = 74) and regional (N = 99) - and for the interaction term of spatial scale with both environmental variables taking local spatial scale as the reference. Multiple R-squared are provided as an indicator of the explained variation of each model.

		Connectance			Overlap			Generality		
		Estimate	T-value	R ²	Estimate	T-value	R ²	Estimate	T-value	R ²
Range in T	Local	0.42	3.115 **	0.53	0.28	2.653 **	0.38	-0.48	-3.170 **	0.23
	Regional	-0.12	-1.237		-0.05	-0.684		0.02	0.223	
	Interaction term	-0.54	-3.237 **		-0.34	-2.536 *		0.51	2.675 **	
Past Climate Change	Local	0.09	1.476	0.51	0.03	0.633	0.35	-0.17	-2.516 *	0.23
	Regional	-0.03	-0.805		-0.01	-0.543		-0.07	-2.077 *	
	Interaction term	-0.12	-1.681 °		-0.05	-0.818		0.09	1.167	

		Vulnerability			Parasitoids			Hosts		
		Estimate	T-value	R ²	Estimate	T-value	R ²	Estimate	T-value	R ²
Range in T	Local	0.68	4.383 ***	0.26	0.32	4.644 ***	0.88	-0.65	-3.675 ***	0.52
	Regional	-0.09	-0.810		-0.03	-0.489		0.12	0.936	
	Interaction term	-0.77	-3.998 ***		-0.35	-4.016 ***		0.77	3.506 ***	
Past Climate Change	Local	0.17	2.421 *	0.20	0.11	3.469 **	0.87	-0.17	-2.198 *	0.49
	Regional	0.009	0.221		0.01	0.838		0.03	-0.722	
	Interaction term	-0.16	-1.997 *		-0.09	-2.606 **		0.14	1.557	

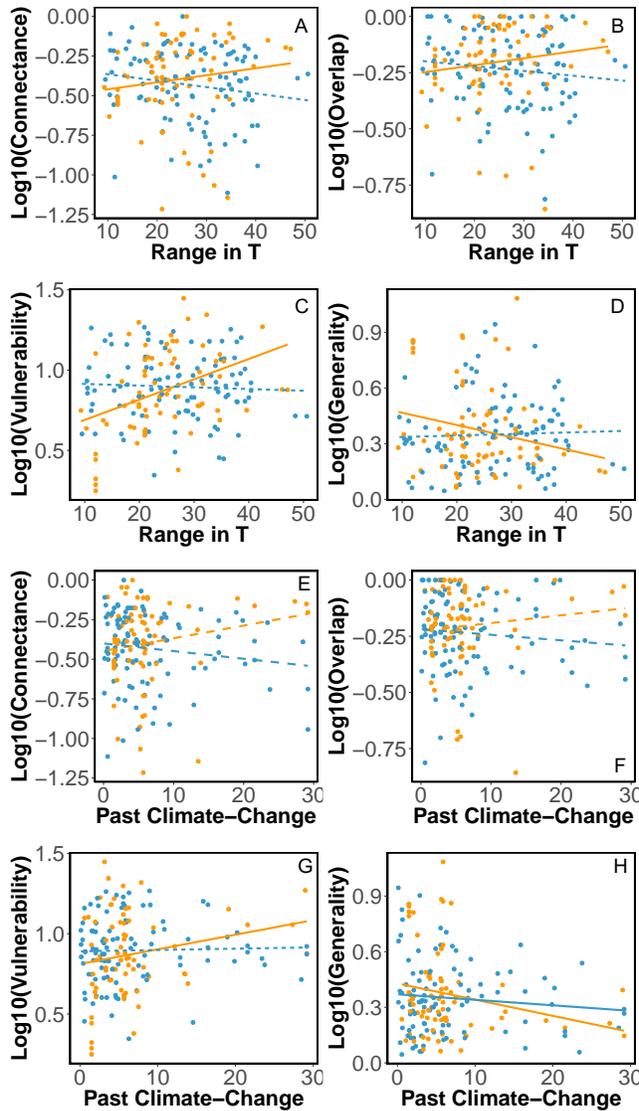


Figure 15. Geographical variation in network structure along the gradient of (a-d) annual temperature range and (e-h) historic climate-change (i.e., change in mean annual temperature for the last 21,000 years). Relationship between network connectance, consumer overlap, resource vulnerability and consumer diet breadth with both environmental variables at local (orange) and regional (blue) spatial scales. Notice that the tendency line in blue for regional spatial scales does not indicate a significant relationship.

These contrasting results can be explained by changes observed in the number of parasitoids and the number of hosts in the local webs along both environmental gradients. While the number of parasitoids increased with temperature range and historical climate-change, the number of hosts decreased (Table 2, Figure 16). For regional networks, neither parasitoid nor host richness changed across the gradients (Table 2, Figure 16). These opposite tendencies for the number of parasitoids and the number of hosts at the local scale indicate that the distribution of the number of species across trophic levels (i.e. consumer:resource ratio) is changing along both gradients of environmental constancy. Thus, in more constant environments, fewer consumers attacked resources, but this pattern was reversed in more fluctuating areas where the number of parasitoids per host was higher and, therefore, prey vulnerability was larger.

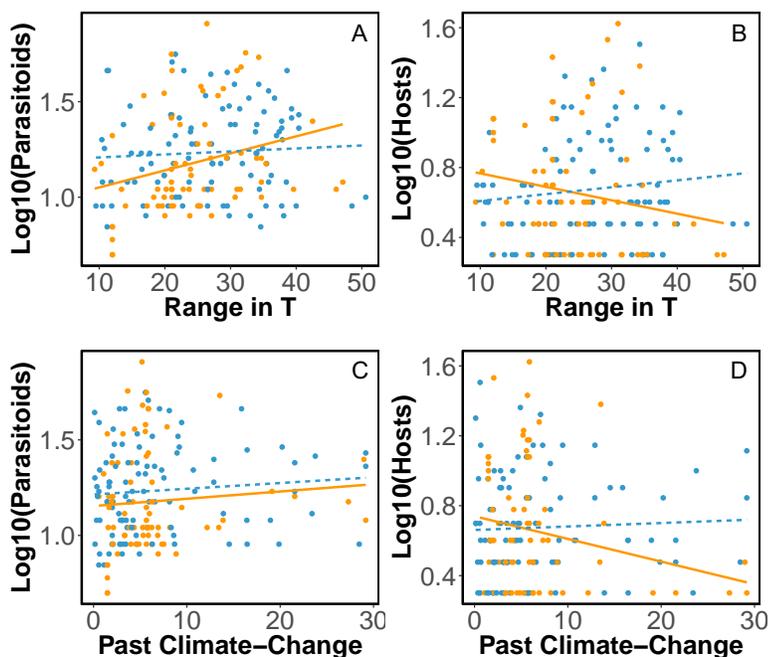


Figure 16. Relationship of the number of parasitoids and hosts with (a and b, respectively) the gradient of annual temperature range and (c, d) the gradient of historic climate-change (i.e. change in mean annual temperature for the last 21,000 years) at both local (orange) and regional (blue) spatial scales. Notice that the tendency line in blue for regional spatial scales does not indicate a significant relationship.

Given that biotic specialization was not well predicted by our environmental variables at the regional scale, the question that remains is: How can the distribution of species richness across trophic levels (i.e., consumer:resource ratio), from which the patterns in vulnerability and diet breadth derive, change from local to regional webs along the gradients of environmental constancy?

1.4.2 Beta-diversity as a potential mechanism

We hypothesize that the difference in β -diversity across trophic levels modulates the changes in network structure from local to regional spatial scales, and that these differences in β -diversity across trophic levels varied along the gradients of environmental constancy. In figure 14 we illustrate this mechanism with two specific examples corresponding to the two extremes of the constancy gradient, one for more climatically constant regions like the Tropics (Figure 14a) and one for more fluctuating regions (Figure 14b). If $\beta_{\text{consumer-diversity}} > \beta_{\text{resource-diversity}}$, we observe changes in network structure from local

to regional spatial scales (Figure 14a). In contrast, similar β -diversity in both trophic levels does not generate differences in network structure across spatial scales beyond those produced by the increase in the number of species (Figure 14b). In figure 17 we extend this example to the whole range of β -diversity values to explore systematically the effects of β -diversity in both trophic levels on the structure of the networks across spatial scales. The larger the difference between $\beta_{\text{consumer-diversity}}$ and $\beta_{\text{resource-diversity}}$, the larger the change expected in network structure across spatial scales (Figure 17a). Conversely, assigning similar values of β -diversity between resources and consumers only generates differences in network structure from local to regional webs due to the general increase in species richness (Figure 17b). In this case, the larger the value of β -diversity, the larger the increase in the number of species as local communities are successively aggregated into the regional network. Our tropical networks appear to display the structural patterns across spatial scales corresponding to the scenario where $\beta_{\text{consumer-diversity}} > \beta_{\text{resource-diversity}}$. Patterns displayed by networks in more fluctuating environments (i.e., temperate and continental), however, suggest that more balanced values, or even inversed, i.e., $\beta_{\text{consumer-diversity}} \leq \beta_{\text{resource-diversity}}$, are predominant.

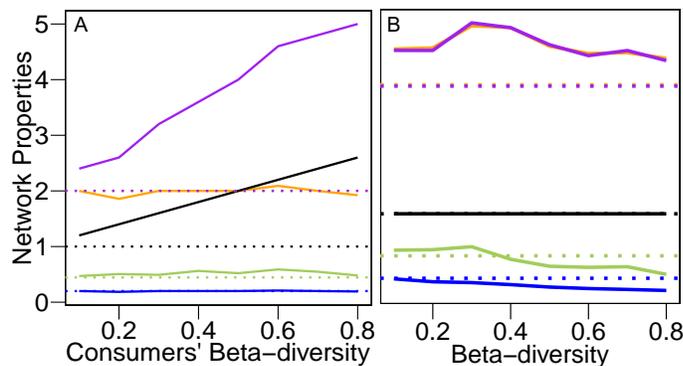


Figure 17. Response of different specialization metrics to increases in (a) consumer beta-diversity (where resource beta-diversity=0) and (b) beta-diversity at both trophic levels increasing simultaneously (i.e., beta diversity of consumers equals that of resources). Dotted lines represent network properties values at the local scale. Continuous lines represent network property values of the aggregated network (i.e., regional scale) as beta-diversity increases. Blue for connectance, green for overlap, orange for diet breadth, purple for vulnerability and black for consumer:resource ratios.

1.5 DISCUSSION

We have shown that the geographical variation of food web structure is scale dependent. In particular, the gradient of biotic specialization is not universal. It depends on both the facet of biotic specialization analysed and the spatial scale of observation. Indeed, local and regional networks displayed very different patterns along the gradients of contemporary and historical climatic constancy. At the regional scale, we found little evidence for the biotic specialization hypothesis for any of the facets analysed. In contrast, the biotic specialization hypothesis generally holds at the local scale: networks in more constant environments were less connected, consumers overlapped less their niches, and preys were attacked by fewer predators. The only facet of specialization that showed the opposite pattern was diet breadth: consumers were more generalists in more constant environments, contrary to the hypothesized latitudinal gradient on niche breadth [34], [63], [119].

Current climatic constancy was a better predictor of biotic specialization at the local scale than historical climatic constancy. Even though past climate stability has been shown to be a good predictor of the structure of plant-hummingbird networks [58], [71], a meta-analysis on pollination networks showed stronger effects of contemporary climate on network specialization [64], in agreement with our findings. Our measure of historical climatic constancy (i.e., difference between current mean annual temperature and mean annual temperature 21.000ybp) allows for a direct comparison with current climatic constancy, as both measures account for the temperature range experienced over long and short temporal scales, respectively. However, it is a coarse-grained measure that does not account for fine-scale climatic fluctuations within the historical period considered. Because species may respond differently to climate changes, climatic fluctuations can disrupt biotic specialization through phenological mismatches or changes in the geographical distributions of species [156]–[158]. Thus, the explanatory power of historical climatic constancy can be smaller than that corresponding to current climatic constancy.

Our results partially agree with previous findings. Dalsgaard and colleagues [74] analysed the latitudinal gradient in biotic specialization of avian plant-frugivore networks from two different perspectives, namely niche partitioning in the network and consumers' dietary specialization, and found opposite results. They showed that network-derived specialization increases with latitude while bird species were more specialized on specific fruit diet in the Tropics. Their results highlight the need of comparing different scales of biotic specialization for a better understanding of a biogeographical pattern. In our case, the analysis of different facets of biotic specialization at different spatial scales was crucial to gain a better understanding of the biogeographical pattern. Interestingly, we found opposite geographical

patterns in biotic specialization between consumer (i.e., generality) and resource (i.e., vulnerability) species (Figure 15). While diet breadth was higher in more climatically constant regions, resource vulnerability was lower. Importantly, the number of consumers and the number of resources also showed opposite trends along both gradients of environmental constancy, which explained the opposite results found between consumer diet breadth and prey vulnerability at the local scale (Figure 16). Therefore, analysing different facets of biotic specialization allowed us to have a broader understanding of the geographical variation of biotic specialization.

In a recent study of the macroecology of pollination networks, Trøjelsgaard and Olesen [72] found that pollinators:plant ratios increased with latitude, indicating that mid-latitudes harboured more pollinators per plants species than communities in the tropics. Our results for antagonistic networks are in agreement with this finding at the local scale where we found that the number of parasitoids decreased with environmental constancy while the number of hosts increased (Figure 16), indicating a decrease of the consumer:resource ratio with environmental constancy. However, at the regional scale, we did not observe a significant change in the number of consumers and resources along neither of the environmental constancy gradients. This results in opposite patterns between both extremes of the gradients when local and regional networks are compared (Figure 15 and Figure 16). In more constant environments, local networks have a smaller proportion of consumers per resources than regional networks. The opposite is true for more fluctuating environments, where local networks have a larger proportion of consumers per resources than regional networks (Figure 16).

1.5.1 The importance of spatial turnover across environmental gradients

One key question remains: How can the same “potential” regional network lead to opposite “realized” local networks along the climatic constancy gradient? More specifically, how can the distribution of diversity across trophic levels have an opposite trend between spatial scales at both extremes of the gradient?

We propose an explanation based on the differences in spatial turnover (i.e., β -diversity, *sensu* Whittaker [130]) of local consumer and resource assemblages along the gradients of climatic constancy. In the tropics (i.e., less fluctuating regions), the spatial turnover of consumers should be larger than that of resources, so that when we aggregate local into regional webs, the number of consumers increases faster than the number of resources (Figure 14, Figure 17). In contrast, in more fluctuating areas the process should be the opposite: larger spatial turnover of resources results in a faster increase in the number of resources at the regional scale. Empirical evidence partially supports our hypothesis. Consumer

assemblages (parasites and parasitoids in particular) tend to be less similar across local communities than resource assemblages (herbivores in particular) [128]. In addition, β -diversity in the tropics tends to be higher than at higher latitudes, at least at relatively small spatial scales [128], [132], [159], [160].

A number of ecological processes can explain why consumers' β -diversity is larger than resources β -diversity in the tropics, but not in more climatically fluctuating environments. This could simply result from stochastic assembly processes from two species regional pools with different richness. If regional consumer diversity is larger in the tropics than in temperate areas, which it is, random assembly processes of local communities would lead to larger compositional dissimilarities of consumers in the tropics [132], [161]. However, other non-stochastic ecological processes can also explain this pattern.

Firstly, consumer assemblage similarity tends to decrease with productivity (e.g, for aquatic consumer insects see [162], [163]), as environmental heterogeneity and reduced dispersal rates among local communities increase. As productivity tends to be positively correlated with thermal stability [30], [164], this might explain the increase of consumer β -diversity towards the tropics.

Secondly, diet generalists tend to have wider geographical ranges than specialized species [31], [165]–[167], and consumers tend to have patchier distributions in the tropics [31], [33], [159], [168]. This reduces the dissimilarity in the composition of local generalist consumer assemblages. Since generalist species prey upon a wide range of resource species, compositional differences among sites on resource assemblages need to be high. This might explain why diet breadth was not well predicted by the gradients of environmental constancy at the regional scale while at the local scale we observed opposite patterns for each extreme of the gradients (Figure 15). Thus, this suggests that the dissimilarity on the composition of local consumer assemblages is higher in the Tropics due to their tendency of having narrower geographical ranges than generalist species [31], [33], [159], [168]. This could lead to the isolation of interactions across space if there were reciprocal specializations between consumers and resources, but reciprocal specializations are extremely rare in nature [118] and in our networks isolated links were not taken into account. Thus, this suggests that the dissimilarity on the composition of resource assemblages among local sites is low, and therefore, resource species are attacked by many consumers with narrower and patchier distributions (see Figure 15).

Thirdly, consumer competitive exclusion can be stronger in the tropics than in temperate areas, ultimately determining the patchier distribution of consumers in the tropics [31]. Although supporting evidence is not unequivocal [169]–[172], local dynamics in the tropics could exclude different consumers

in different habitat patches, resulting in more specialized and less similar consumer communities across patches. Our results show that consumers segregated their dietary niches more in more constant environments (less consumer overlap) (Figure 15). This could be the consequence of more intense competitive exclusion, so that, locally, for consumers to coexist, they should overlap their dietary niches only weakly [173].

1.5.2 Conclusions and perspectives

Our study is not the first attempt to examine network structure across biogeographical scales. However, it is the first to explore the spatial scale-dependency of network patterns across large biogeographical gradients. We found that the difference in the consumer:resource ratio across spatial scales changes along the biogeographical gradient of environmental constancy which generates further changes in network structure. Our results thus identify a geographical gradient of biotic specialization that depends both on the spatial scale of observation and on the facet of specialization of interest. They highlight that the spatial patterning of diversity across trophic levels, summarized in β -diversity, is key to understand the geographical gradient of biotic specialization. Similarly, our results show the importance of considering different spatial scales to get a broader understanding of the specialization pattern and their determinants. Additionally, if network structure varies across spatial scales [96], [103], [110], [124], then network studies estimating the causes of variation in network structure along any environmental gradient [77], [174], [175] might benefit from understanding the spatial scaling of network structure along the gradient. However, caution must be exerted when interpreting the comparison between different spatial scales. Regional networks account for all the interactions between consumers and resources that occur in at least one locality of the area sampled, and thus it does not require that the observed interaction is realized in every location of the area considered. Therefore, network structure at the regional scale must be understood as the structure of the potential network of interactions at a given area, which together with the information on the structure of the realised network at the local scale can help to elucidate the role of different spatial processes in a given region.

Further theoretical and empirical research is needed to determine how general our findings are in regards to the scale-dependency of network structure across large environmental gradients and across different study systems. We focused on host-parasitoid networks which have been described as a particular group of antagonistic interactions that are considered to have higher levels of consumer specialization than other antagonistic networks [8], [176]. However, the results presented here and the mechanisms proposed to explain the changes in network structure across spatial scales should hold for

any system whose consumers are not super generalists and that it presents a minimum degree of spatial turnover. Regardless of the type of interaction, unbalanced values of β -diversity across trophic levels should generate changes in network structure across spatial scales. Future studies should aim to quantify the spatial scaling of network structure in a continuous way along environmental gradients to better understand what is the role of β -diversity in determining the possible differences in network structure across spatial scales in different parts of the world.

Acknowledgements:

This work was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41 and 394 ANR-11-IDEX-002-02), and by a Region Midi-Pyrenees project (CNRS 121090).

Authors contributions:

NG, BH and JMM designed research; NG and JMM conducted research; NG and JMM wrote the paper; All authors edited the paper.

SUPPLEMENTARY MATERIAL CHAPTER 1

Content

- **Table S1.1.** Relationship of all network properties with the number of species.
- **Table S1.2.** Relationship of the number of species with the climatic predictive variables
- **Table S1.3.** Statistical models with the number of species at each trophic level as independent covariates.
- **Figure S1.1.** Relationship of the number of species richness with all network properties.
- **Figure S1.2.** Relationship of the number of species with annual temperature range and past climate-change.

Table S1.1. GLM results for the relationship of each network property with number of species. Estimates, T values and statistical significances (***) for p-values<0.0001; ** for p-values<0.01; * for p-values<0.05; ° for p-values<0.1) are indicated for the relationship at each spatial scale - local (N = 74) and regional (N = 99) - and for the interaction term of spatial scale with both environmental variables taking local spatial scale as the reference. Notice that to analyse the relationship of the number of parasitoids and the number of hosts with species richness, we additionally analyse the consumer:resource ratio.

		Connectance		Overlap		Generality		Vulnerability	
		Estimate	T-value	Estimate	T-value	Estimate	T-value	Estimate	T-value
Number of Species	Local	-0.78	-9.660 ***	-0.41	-6.306 ***	0.44	4.812 ***	0.37	3.905 ***
	Regional	-0.73	-9.307 ***	-0.46	-7.272 ***	0.38	4.314 ***	0.41	4.443 ***
	Interaction term	0.05	0.498	-0.05	-0.505	-0.06	-0.472	0.04	0.271

		Parasitoids		Hosts		C:R ratio	
		Estimate	T-value	Estimate	T-value	Estimate	T-value
Number of Species	Local	0.97	21.906 ***	0.99	8.996 ***	-0.01	-0.081
	Regional	1.01	23.484 ***	0.90	8.553 ***	0.08	0.557
	Interaction term	0.04	0.595	-0.08	-0.514	0.09	0.446

Table S1.2. GLM results for the relationship of species richness with the predictor variables of environmental constancy. Estimates, T values and statistical significances (** for p-values<0.01; * for p-values<0.05; ° for p-values<0.1) are indicated for the relationship at each spatial scale - local (N = 74) and regional (N = 99) - and for the interaction term of spatial scale with both environmental variables taking local spatial scale as the reference.

		Number of species	
		Estimate	T-value
Annual Range in T	Local	0.24	1.344
	Regional	0.14	1.051
	Interaction term	-0.10	-0.448
Past Climate- Change	Local	0.05	0.065
	Regional	0.03	0.738
	Interaction term	0.03	0.306

Table S1.3. GLM results for the relationship of each network property with annual temperature range and past climate-change considering the number of hosts and parasitoids as independent covariates. Estimates, T values and statistical significances (** for p-values<0.01; * for p-values<0.05; ° for p-values<0.1) are indicated for the relationship at each spatial scale - local (N = 74) and regional (N = 99) - and for the interaction term of spatial scale with both environmental variables taking local spatial scale as the reference. Multiple R-squared are provided as an indicator of the explained variation of each model.

		Connectance			Overlap			Generality			Vulnerability		
		Estimate	T-value	R ²	Estimate	T-value	R ²	Estimate	T-value	R ²	Estimate	T-value	R ²
Range in T	Local	0.33	3.053 **	0.71	0.30	2.951 **	0.49	-0.3	-2.533 *	0.55	0.46	4.078 ***	0.64
	Regional	-0.07	-0.874		-0.02	-0.341		-0.04	-0.551		0.03	0.330	
	Interaction term	-0.40	-2.982 **		-0.32	-2.586 *		0.25	1.722 °		-0.43	-3.101 **	
Past Climate Change	Local	0.06	1.279	0.70	0.03	0.695	0.47	-0.11	-2.124 *	0.55	0.08	1.566	0.61
	Regional	-0.07	-2.470 *		-0.04	-1.602		-0.04	-1.319		-0.03	-0.915	
	Interaction term	-0.13	-2.327 *		-0.07	-1.390		0.07	1.203		-0.11	-1.813 °	

Figure S1.1. Relationship of the number of species richness with all network properties analysed, at both local (orange) and regional (blue) spatial scales. Importantly, the slope of the relationship between connectance and the number of species is -0.645 at local scale and -0.788 at regional scale, suggesting that S-C relationships are between the link species scaling law and the constant connectance hypothesis.

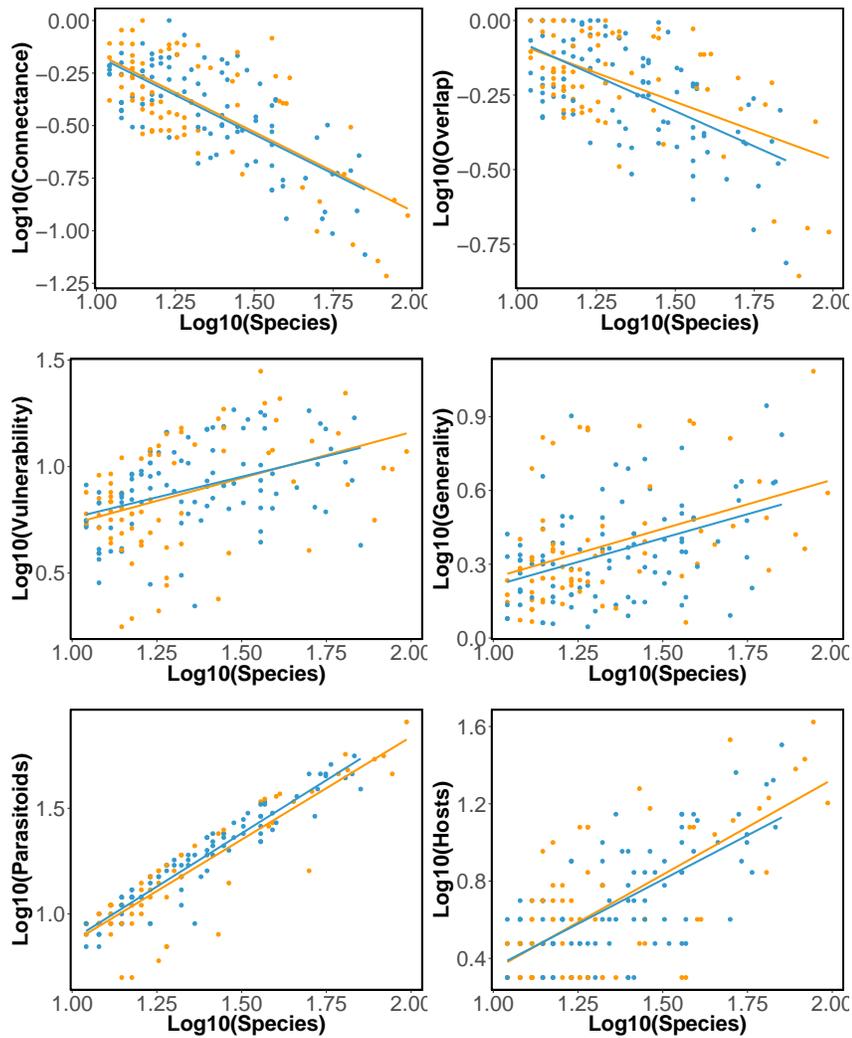
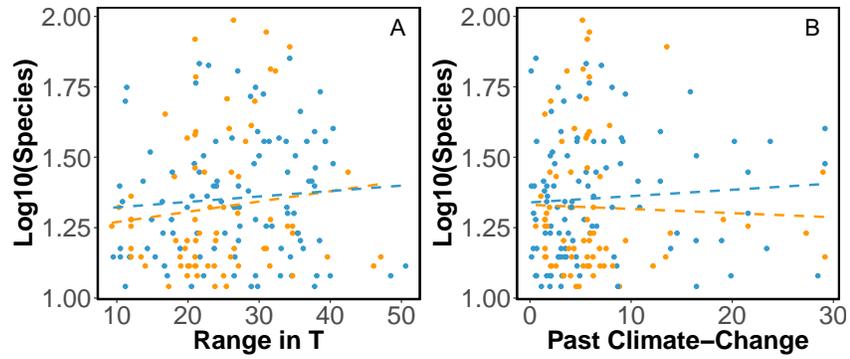


Figure S1.2. Relationship of the number of species with (a) Annual temperature range and (b) Past climate-change, at both local (orange) and regional (blue) spatial scales. Notice that tendency lines do not indicate a significant relationship.



Chapter 2

EFFECTS OF AREA SIZE ON NETWORK STRUCTURE: THEORETICAL APPROACH

2.1 TITLE OF THE SCIENTIFIC ARTICLE:

*The spatial scaling of species interaction networks*³

Keywords: community structure, ecological networks, spatial food webs, species-area relationship, network-area relationship, metacommunities.

ABSTRACT

Species-Area Relationships (SARs) are pivotal to understand the distribution of biodiversity across spatial scales. We know little, however, about how the network of biotic interactions in which biodiversity is embedded changes with spatial extent. Here we develop a new theoretical framework which enables us to explore how different assembly mechanisms and theoretical models affect multiple properties of ecological networks across space. We present a number of testable predictions on network-area relationships (NARs) for multi-trophic communities. Network structure changes as area increases because of (1) the existence of different SARs across trophic levels, (2) the preferential selection of generalist species at small spatial extents, and (3) the effect of dispersal limitation promoting beta-diversity. Developing an understanding of NARs will complement the growing body of knowledge on SARs with potential applications in conservation ecology. Specifically, combined with further empirical evidence, NARs can generate predictions of potential effects on ecological communities of habitat loss and fragmentation in a changing world.

³ This article represents a collaboration with Miguel Lurgi, Bernat Claramunt, Marie-Josée Fortin, Shawn Leroux, Kevin Cazelles, Dominique Gravel and José M. Montoya. It is published in Nature Ecology and Evolution: **Galiana, N. et al.** The spatial scaling of species interaction networks. *Nat. Ecol. Evol.* **2**, 782–790 (2018). DOI: 10.1038/s41559-018-0517-3

2.2 INTRODUCTION

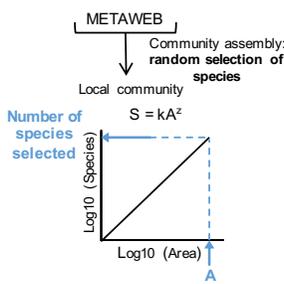
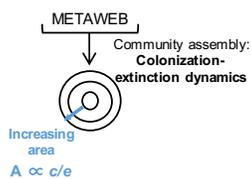
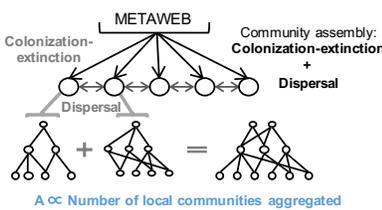
The species-area relationship (SAR) is amongst the most widely recognised ecological patterns [79], [81], [83]. The larger the geographical area sampled, the richer is the ecological community [80], [81], [83]. SARs have been used extensively to estimate species richness in a given region [80], [81], [177], and to predict species extinctions due to habitat loss [178]–[180]. Yet, for several logistic reasons, most studies of species-area relationships have been traditionally limited to particular taxa and functional groups. SARs for multi-trophic communities are just starting to be documented [95]–[97] along with the role played by biotic interactions in shaping these relationships [96], [98].

Biotic interactions modulate the outcomes of community assembly and disassembly. Different spatial processes in turn determine which interactions will be realized, ultimately regulating community dynamics [86], [120], [122], [181]. For example, higher dispersal rates of species at the top of the food web can increase the proportion of top predators in local communities and in turn enhance top-down regulation [122], [182]. The relationship between area and biodiversity is thus inherently affected by the way ecological interactions and the emerging network structure of multispecies communities change according to the location and size of the area sampled. Unveiling the mechanisms underlying the relationship between area and biotic interactions will provide insights on ecosystem organization across spatial scales [96], [103], [109], [110], [181], [183].

Gaining a deeper understanding of network-area relationships (NARs) is arguably as important as the knowledge we have on SARs. Indeed, understanding the mechanistic basis of the spatial scaling of network properties is essential to predict the effects of disturbances such as habitat loss and fragmentation on the organisation of multispecies communities, ultimately affecting their persistence and functioning. Disentangling how network structure changes with spatial scale is crucial to interpret empirical data on ecological networks. If the spatial scale affects network structure, then comparative studies should explicitly consider the area sampled as well as the environmental conditions to generate meaningful conclusions, as it is systematically done on studies on diversity distribution patterns [111].

Here we propose NARs as a theoretical and predictive framework to study the variation of the properties of ecological networks (e.g., connectivity, trophic level composition, trophic chain length) across spatial scales; from small to large areas. We first showcase a number of spatial processes (e.g., dispersal) that could generate different types of NARs. Then we present three simple theoretical models to understand and test how NARs could emerge given specific processes of spatial assembly of multi-trophic communities. As such, we provide new insights on the role of spatial processes on community

assembly and structure and explain how this can be used to predict not only the effects of habitat loss and fragmentation on species richness across trophic levels, but also on the structure of biotic interactions. Last, we propose further theoretical and empirical research avenues, stemming from our NARs framework, which could contribute to a unified theory of the spatial scaling of ecological communities.

Box 1 A mechanistic approach to understand Network-Area relationships (NARs).			
Model used	Trophic Sampling	Trophic Theory of Island Biogeography	Trophic Meta-community
Process tested	The effect of Species-Area Relationship (SAR) on the spatial scaling of network structure.	Extinction probability (e) decreases with Area size promoting a general increase in species richness.	Dispersal limitation increases spatial heterogeneity in species composition (i.e., beta-diversity).
Underlying mechanisms for NARs	The added effect of the scaling of the number of links with species richness and the variation of SARs across trophic levels.	Larger species richness in larger areas favours the opportunity for all consumers (not only generalists) to find a prey. This promotes a preferential selection of generalist species in smaller areas that will generate changes in network structure across spatial scales.	The higher the heterogeneity in species composition across space, the stronger dependency of network structure with area: increasing the area sampled increases the number of new species sampled and has a stronger effect on network properties.
	 <p>Number of species selected</p> <p>Log10 (Species)</p> <p>Log10 (Area)</p> <p>$S = kA^z$</p>	 <p>Increasing area</p> <p>$A \propto c/e$</p>	 <p>Community assembly: Colonization-extinction + Dispersal</p> <p>Dispersal</p> <p>$A \propto \text{Number of local communities aggregated}$</p>
Model description	The <i>Trophic Sampling model</i> subsamples species randomly from the regional pool of 200 species (metaweb). It uses the species – area relationship ($S = kA^z$; with $k = 10$ and $z = 0.27$) to obtain the number of species expected for a given area and, therefore, to construct food webs of different sizes that correspond to different areas. Local community assembly is only constrained by trophic interactions, i.e., consumers need a prey to be selected.	The <i>Trophic Theory of Island Biogeography</i> assumes that species from the mainland (metaweb) can colonise the island with a fixed colonisation probability (c) and can go extinct with a range of extinction probabilities (e). Stochastic colonisation-extinction dynamics are trophically constrained. That is, consumers need to have a prey on the island to be able to colonize, and they go extinct if their last prey goes extinct. Area is determined by the ratio between colonization and extinction (c/e).	It consists in 75 local patches connected to the mainland (metaweb) and connected to themselves depending on the distance. Species can arrive to each local patch from the metaweb with a fixed colonisation probability and can go extinct with a fixed probability. Species can disperse between connected local patches according to different dispersal values. Stochastic colonisation-extinction dynamics and dispersal are trophically constrained. Area is determined by the aggregation of local communities (patches) in an ever-increasing fashion from 1 to the maximum number of communities (75).

Mechanisms behind Network-Area Relationships

There are several possible mechanisms responsible for changes of network structure across spatial scales. Box 1 provides a synthesis of the ones analysed here, our expectations for the emergence of NARs based on three mechanisms, and the theoretical models used to evaluate our expectations.

1. The first mechanism is derived from the SAR. There is an associated increase in the number of interactions (links) with the increase of species richness with area. Two major hypotheses have been proposed to account for the variation of the number of links with species richness in food webs. Both hypotheses do not explicitly account for species-area relationships. The ‘link-species scaling law’ [104] states that species interact with a constant number of species independently of species richness [105], [106]. In contrast, the ‘constant connectance hypothesis’ [107] states that the fraction of potential interactions realized (i.e., the number of trophic links L , standardized by the number of potential interactions S^2) is constant across food webs, irrespective of species richness. Empirical evidence suggests that link-species richness relationships lay in between the two hypotheses [108], [184]. If we introduce area within these link-species scaling hypotheses, given that S increases with area, and L scales with S , we expect changes in food web structure with area simply emerging from SAR which are in turn shaped by the specific link-species relationship in place. Brose and colleagues [109] proposed a scaling of trophic links with area by combining species–area and the link–species scaling theories mentioned above. Following their approximation, we generated trophic communities of different sizes (i.e., different number of species) with the *Trophic Sampling* model. This model randomly subsamples species from the metaweb (i.e., food web of 200 species generated with the niche model [185], see Supplementary Methods and Supplementary Table 2.1 for a full description), which conforms the regional pool of species, with the only constraint that each consumer needs at least one prey to be selected (Box 1). We expect different shapes of the species richness–area relationships at each trophic level emerging from this trophic constraint. If the spatial scaling of species richness differs among trophic levels, different facets of network structure are expected to change with area. As a consequence, the proportion of species belonging to each trophic level (e.g., basal, intermediate, and top species) will be different at each spatial scale, triggering further consequences on community structure [88], [95], [96]. We explore the combination of both mechanisms (i.e. the scaling of the number of links with species richness and the variation of SARs across trophic levels) with the *Trophic Sampling* model (Box1; Supplementary Methods).

2. The second mechanism arises from the scaling of colonization-extinction dynamics in multi-trophic communities with area. This was first considered in the Theory of Island Biogeography [80] (hereafter *TIB*)

and its extension to trophic interactions [86]–[88], [93] (Trophic Theory of Island Biogeography, *TTIB*). The *TIB* predicts the richness of local assemblages from the equilibrium between colonisation and extinction processes. It assumes that the closer the island is to the mainland the larger the colonisation rate [80], and that the larger the island size the lower the extinction rate due to the increase in population sizes [84], [85]. The *TTIB* incorporates a trophic constraint not considered in the *TIB*: consumers must have a prey on the islands they colonize to be able to establish and persist. Therefore, the richness of the local assemblage and their biotic interactions are defined by the equilibrium between colonisation and extinction processes where species that are diet generalists and/or belong to lower trophic level species are preferentially selected given that they are less affected by the trophic constraint. Generalist species have been shown to be faster colonizers than specialists, ultimately shifting community structure through time [86], [186]. We expect stronger impact of this trophic constraint at smaller areas, where the number of species is smaller. As area increases, the number of species also increases, which in turn increases the opportunity for consumers to find a prey, and therefore not only generalist species will be able to colonize, but also specialists, ultimately promoting changes in network structure as area changes. We use the *TTIB* model [86] to generate islands of different sizes based on different colonisation/extinction ratios where colonization rate is fixed to analyse the network structure resulting from the assembly process for each island size (Box 1; Supplementary Methods).

3. The last mechanism arises from the spatial variability in community composition, i.e., spatial turnover of species. Clumping of species underlies beta-diversity and SARs [187], [188]. Its effect on the variation of network structure with area is driven by the increase in the number of species and their interactions as area increases. The spatial turnover of species composition can be explained by several processes [128]. Here we focus on the spatial configuration and connectivity of the landscape, which ultimately determines the rates of dispersal of organisms between sites. In fragmented landscapes with major dispersal barriers, species turnover is higher than in homogeneous and continuous environments [189]. Changes in network structure with area are likely to be mediated by dispersal limitation through its effects on spatial turnover. Larger beta-diversity values will generate larger changes in network structure with area because the number of different species encountered as the area sampled increases will be larger. To test the effects of this process we employ a multi-trophic meta-community model, extending the above-mentioned *TTIB* to entire landscapes, where we control species dispersal between local patches (Box 1; Supplementary Methods).

2.3 RESULTS

2.3.1 Multi-trophic community assembly models

We explore the effects of each process on the spatial scaling of food web structure with the three models of multi-trophic community assembly mentioned above. We then analyse several network properties at different spatial scales, which allows us to characterize a suite of NARs (see Supplementary Methods for a full description of the assembly models and the network properties used). In this section, we first present the emergence of the mechanisms tested for each assembly model and its effects on the spatial scaling of food web structure. We then provide a comparison between the predictions emerging from each model.

Trophic Sampling model

Mechanisms. The number of links scales exponentially with species richness (Slope= 1.91 ± 0.003 - 95% confidence interval- in log-log space; Figure 18a). Although the relationship falls between the two link scaling hypotheses (link-species scaling law -Slope ≈ 1 in log-log space- and constant connectance hypothesis -Slope ≈ 2 in log-log space-), our results better support the latter. Additionally, we observe different SARs across trophic levels (Figure 18b). The number of intermediate species increases significantly faster with area than the number of top and basal species (See Supplementary Table 2.2 for statistical analyses). Taken together, these results show that both mechanisms suggested as possible drivers of NARs: (i) link scaling and (ii) different shape of the SARs across trophic levels, are at play in the *Trophic Sampling* model. As expected, these mechanisms trigger changes in network structure from local to regional scales.

NARs. Network complexity properties smoothly increase with area (Figure 19a-b, Supplementary Figure 2.1 and Supplementary Table 2.3). Whereas number of species, links per species, mean indegree and mean outdegree (i.e., mean generality and mean vulnerability, respectively) show a pronounced sub-linear increase quickly approaching the asymptotic value set by the regional network, total number of links increases linearly with area. As a consequence, due to its quadratic relationship with the number of species ($C=L/S^2$), connectance decays sharply with area. That is, network complexity increases with area because larger areas have more species, more links and more links per species. However, given the faster rate of increase in the number of species than in the number of links, we observe a decrease in connectance.

Network vertical diversity properties increase with area (Figure 19c, Supplementary Figure 2.1 and Supplementary Table 2.3). Mean food chain length (MFCL), fraction of omnivory, and fraction of intermediate species increase sharply with area, reaching the asymptote corresponding to the regional values at relatively small areas. This, in turn, decreases asymptotically the fraction of basal and top species with area. Notice however that the fraction of herbivores (included within the category of intermediate species) decreases asymptotically with area, in parallel to the decrease on the fraction of basal species (Supplementary Figure 2.2).

Unexpectedly, network modularity and the distribution of food web motifs do not show strong variations across spatial scales (Figure 19d and Supplementary Figure 2.1). Modularity, the proportion of simple chains, and apparent competition slightly decrease with area while the proportion of exploitative competition shows a small increase with area.

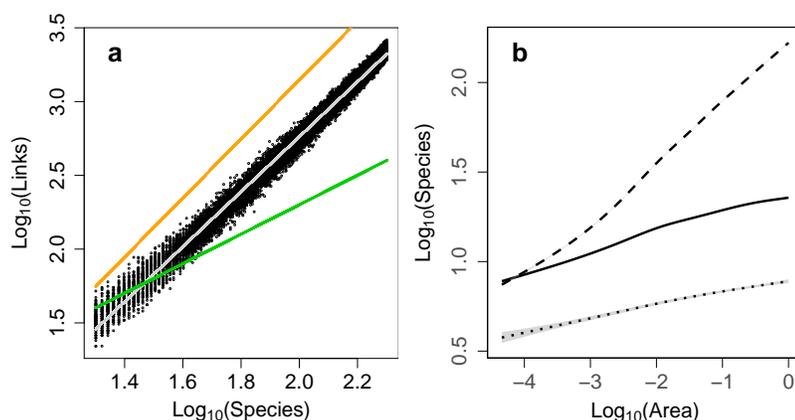


Figure 18. Mechanisms underlying NARs. a) Scaling of the number of links with species richness. Orange line: Constant Connectance Hypothesis (CCH; that is, the number of links in a web increases approximately as the square of the number of trophic species: $L \approx S^2$); Green line: Links Species Scaling Law (LSSL; the number of links per species in a web is constant and scale invariant at roughly two: $L \approx 2S$); Grey line: links-species relationship for the *Trophic Sampling* model. b) Species-Area relationships (SARs) per trophic level for the *Trophic Sampling* model. Area values close to -4 correspond to local communities and values close to 0 correspond to regional communities. Notice that area was rescaled to fall in the range between 0 and 1 , where 0 is the smallest local scale and 1 is the largest regional scale and these are the log-transformed values of area. Black line: basal species; Dashed line: intermediate species; Dotted line: top species. Shaded areas correspond to 95% confidence intervals.

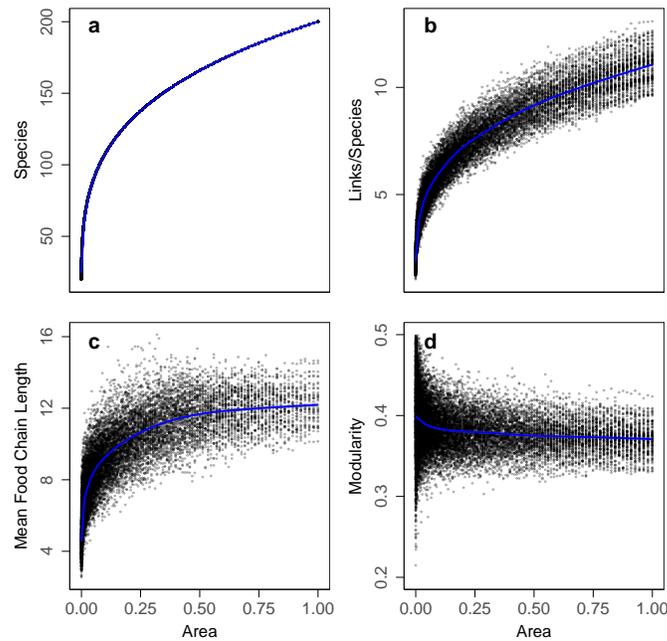


Figure 19. Network-Area relationships (NAR) for the *Trophic Sampling* model. Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. Relationship of (a) the Number of Species, (b) the Number of links per species, (c) Mean food Chain Length and (d) Modularity with Area. Notice that the Species-Area relationship shown in (a) is given by $S = kA^z$, with $k = 10$ and $z = 0.27$. Lines represent a GAM fit to data points.

Trophic Theory of Island Biogeography (TTIB) model

Mechanisms. The proportion of specialist species increases with area (Figure 20a-b). This indicates that species feeding on a larger number of prey do persist better in small patches than specialist species. Potential indegree distributions (quantified as the species indegree in the metaweb) are consequently shifted towards smaller values with increasing area (Figure 20b). Interestingly, this preferential selection of generalist species at smaller scales does not affect the shape of the realized cumulative indegree distributions of the local networks (Figure 20c). Independently of island size, indegree distributions are skewed, i.e., there are more specialist than generalist species in all networks regardless of area. However, it is important to notice that the most specialized species (pointed with arrows in Figure 20c) on small islands have more prey (i.e., they are more generalist) than the most specialized species on large islands. In other words, at smaller areas, we observe a preferential selection of species that are generalists in the

regional pool. As area increases, more specialized species are able to persist, which manifests both in a reduction on mean potential indegree and higher specialization of the most specialised species.

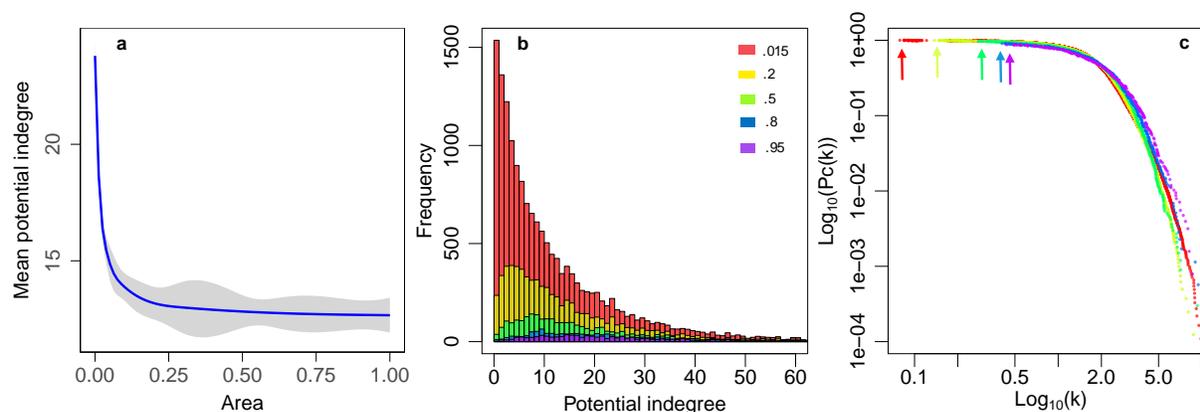


Figure 20. Specialism across spatial scales. a) Variation of food web mean potential indegree -quantified as the species indegree (i.e. generality) in the metaweb- with area for the *TTIB* model. Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. Shaded areas show 95% confidence intervals. b) Species potential indegree distributions for islands of different sizes simulated as the ratio between colonisation and extinction rates, with higher ratios representing larger island areas. Colonisation rate is fixed at 0.2 and each colour represents a different value of extinction (i.e., red and purple correspond to the largest and the smallest area respectively). c) Realised indegree distributions across spatial scales for the *TTIB* model. The cumulative probabilities $P_c(k)$, for $\geq k$, where $P(k)$ is the probability a species has k prey in the network, is represented normalized by the mean number of links per species in the network. Coloured arrows show the starting point of the distribution for each island size. Colours correspond to the same area sizes as in b.

NARs. *TTIB* predictions do not differ qualitatively from the *Trophic Sampling* model. All facets of network complexity increase with area sub-linearly (Supplementary Figure 2.3 and Supplementary Table 2.3), except from connectance, which decreases with area. As for the *Trophic Sampling* model, the faster rate of increase in the number of species than in the number of links, causes the decrease in network connectance even though the number of links per species also increases. In terms of vertical diversity, we observe a sharp increase in omnivory, mean food chain length, and fraction of intermediate species (but see Supplementary Figure 2.2), whereas the fraction of basal and top species show a drastic drop with increasing area (Supplementary Figure 2.3 and Supplementary Table 2.3). Network properties of communities assembled with the *TTIB* model show more abrupt changes with area than the *Trophic Sampling* model, with asymptotes of all food web properties reached at smaller areas. The difference

between the *TTIB* and the *Trophic Sampling* models lays on the complexity of the assembly process. The stochastic nature of the community assembly enforced by the *TTIB* model, which is the result of colonisation-extinction dynamics, favours the persistence over time of generalist consumers. Specialist consumers that depend on a single resource are more prone to become secondarily extinct given the trophic constraint: if their only resource goes stochastically extinct, they go extinct too. In contrast, the *Trophic Sampling* model only searches for possible configurations of a given number of species where every consumer needs to have a resource, without subjecting the selected community to additional stochastic extinctions. Therefore, the effects of the trophic constraint become more evident in the *TTIB*.

The modular structure and the distribution of motifs of the communities are again not strongly affected by the spatial scale (Supplementary Figure 2.3 and Supplementary Table 2.3). Modularity is constant across spatial scales. However, the proportion of simple chains and apparent competition slightly decrease with area while the proportion of exploitative competition increases.

Trophic Meta-community model

Mechanisms. Dispersal limitation among local patches affects the turnover of species composition in our meta-communities. Beta-diversity decreases with dispersal rate (Supplementary Figure 2.4), having further consequences for the spatial scaling of network structure. High dispersal rates increase local diversity (i.e., scaled area 0) and reduces beta-diversity (Supplementary Figure 2.4), making food webs more similar across the landscape. This implies that the amount of change in network structure is smaller, and that the asymptote that corresponds to regional network properties is reached at even smaller areas than for low values of dispersal. As a consequence, for high values of dispersal, we need to aggregate a smaller number of local communities to recover the structure of the large metaweb than with low dispersal rates and with the *TTIB*.

NARs. At low dispersal rates, network-area relationships are similar to those observed for the *TTIB*. Both network complexity and vertical diversity change with area at a smaller rate than compared with the high dispersal scenario (Supplementary Figure 2.5 and Supplementary Table 2.3). High levels of dispersal among local communities weaken the scale-dependency of network structure: increasing the area sampled has less effect on network properties at high levels of dispersal because the values of the properties of the regional network (i.e., the asymptote) are reached earlier. Dispersal increases food web complexity (i.e. more species, links and links per species) and its vertical diversity at both local and regional scales (Supplementary Figure 2.5 and Supplementary Table 2.3).

As for the previous two models, network modularity and the distribution of motifs show small variations across spatial scales for both dispersal levels, being slightly less pronounced for high dispersal levels (Supplementary Figure 2.5). Network modularity, the proportion of simple chains and apparent competition show a marginally decrease with area while the proportion of exploitative competition shows a small increase.

2.3.2 Comparison between models

We found both quantitative and qualitative differences among NARs resulting from the three models (Figure 21, Supplementary Table 2.3 and Supplementary Figure 2.6). Qualitatively, the *Trophic Sampling* model shows smooth changes in network structure with area. The changes in network structure observed with the *TTIB* will be more abrupt as area increases reaching the asymptote faster. Similarly, the *Trophic Meta-community* model with low dispersal leads to abrupt changes in network structure with area. However, important qualitative differences exist between the two that allow for determining the most likely mechanism behind empirical patterns of network scaling (Box 2, Supplementary Figure 2.6). Finally, the *Trophic Meta-community* model with high dispersal shows the smallest change in network structure with area reaching the asymptote for the regional network very small spatial scales.

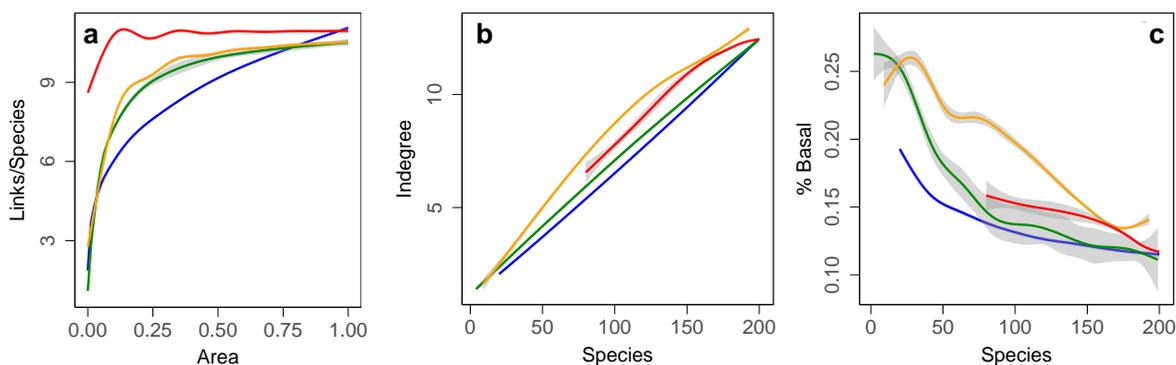


Figure 21. Comparison between models. In (a) variation of the number of links with area for the three different models of community assembly. Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. In (b) and (c) comparison between models controlling by the number of species. For a given number of species, differences in network properties between models. Blue line: *Trophic Sampling* model; Green line: *Trophic theory of Island Biogeography*; Red line: *Trophic Meta-community* model $d=0.01$; Orange line: *Trophic Meta-community* model $d=0.1$. Notice that high dispersal rates in the *Trophic Meta-community* model increase local diversity resulting in local communities with more than 70 species. Lines represent a GAM fit to data points. Shaded areas show 95% confidence intervals.

Quantitatively, the *Trophic Sampling* model shows the lowest rate of growth (g , measured as the steepness of a bounded exponential fitted to the data; Supplementary Table 2.3) for all complexity properties, followed by the *Trophic Meta-community* model with low dispersal, the *TTIB* and lastly the *Trophic Meta-community* model with high dispersal. This implies that increasing the area sampled has a less abrupt effect for NARs in the *Trophic Sampling* model, but this effect is manifested over a larger range of areas sampled. At the other extreme of the spectrum, the *Trophic Meta-community* model with high dispersal shows a rapid change in network structure at relatively small spatial scales. Hence, the scale-dependency of network structure depends on whether we focus on the rate of change of a given network property for a given increase in area, or on the range of areas across which the property changes.

The *Trophic Meta-community* model with low dispersal has the lowest growth rate for most vertical diversity properties, followed by the *Trophic Sampling* model. Whereas the *TTIB* shows the highest growth rate for the proportion of basal and intermediate species, the *Trophic Meta-community* model with high dispersal shows the highest values for the proportion of top species and MFCL (Supplementary Table 2.3). We compared each model with its non-trophic constrained version in Supplementary Figure 2.7. The comparison shows a faster initial increase in complexity for communities assembled using the unconstrained versions of the *TTIB* and the *Trophic Meta-community* model with a levelling off for larger areas, while the unconstrained version of the *Trophic Sampling* model only shows differences for vertical diversity metrics (Supplementary Figure 2.7).

2.4 DISCUSSION

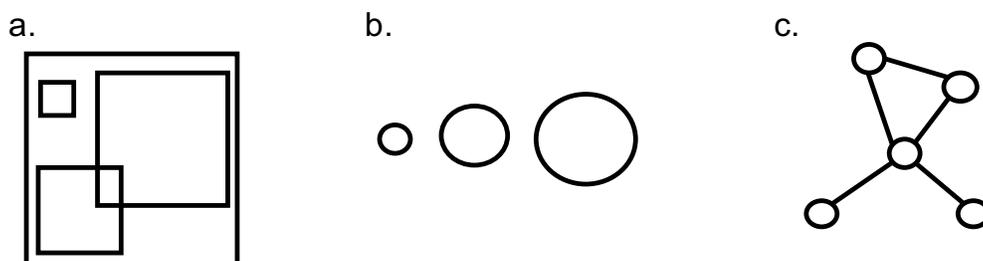
2.4.1 Testable predictions

We presented a theoretical framework predicting the existence of a number of network-area relationships (NARs) in spatial multi-trophic communities, arising from different assembly processes. Although we obtained some universal predictions independent of the particularities of the assembly process used, we found differences in regards to the exact shapes of the specific NAR under scrutiny. This allows for specific predictions emerging from each model to be tested with empirical data (Boxes 2 and 3). In particular, we showed that the existence of different SARs across trophic levels has consequences for the variation of network structure with increasing area, that the preferential selection of generalist species at small areas causes drastic changes on network structure in space, and that dispersal limitation is a key process influencing trophic interactions across spatial scales. Here we summarize and discuss a number of empirically testable predictions emerging from our framework (Boxes 2 and 3), and provide

suggestions on where to focus future research efforts to better understand the causes and consequences of the variation of network structure across spatial scales.

Box 2 Empirical data and testable predictions

Each model used could be represented by a different empirical dataset. The *Trophic Sampling* model (a) corresponds to random subsamples of different area sizes all included within a larger homogeneous area. The *Trophic Theory of Island Biogeography* model (b) corresponds to independent and isolated islands (or patches) of different sizes (e.g., an archipelago). The *Trophic Metacommunity* model (c) corresponds to independent local communities (e.g., patches, islands) of the same size connected through dispersal, where the spatial scaling of network structure is given by the progressive aggregation of different localities.



We can predict a different scaling of network structure in space emerging from each type of data (figure 21). When area is subsampled randomly, network structure will smoothly change as we increase the size of the area sampled. In isolated islands, where each island constitutes one fully assembled community, changes in network structure will be more abrupt as area increases reaching the asymptote faster. In metacommunities, the spatial scaling of network structure will be determined by the spatial heterogeneity in species composition. In fully connected metacommunities (i.e., high dispersal), changes in network structure with area will be minimal. In poorly connected metacommunities (i.e., low dispersal), the spatial scaling of network structure will resemble the one observed in isolated islands.

We provide two illustrative predictions for two different datasets. One belonging to islands within an archipelago, another one to local habitats connected to each other within a landscape. We expect the number of links per species to increase much faster for the archipelago and for the landscape with poor connectivity among patches. However, for a landscape with high connectivity and low dispersal limitations, the increase in the number of links with species will be minimal. Similarly, the mean number of links needed to get from the basal species to the top species (Mean Food Chain Length) will increase with area much faster in archipelagos and in poorly connected landscapes than in landscapes where there is no dispersal limitation.

Box 3 Universal predictions**Network Complexity**

Network Degree distribution preserves its skewness across spatial scales, but specialism increases with area.

Indegree distributions are skewed regardless of area, i.e., there are more specialist than generalist species in all networks irrespective of the spatial scale (Figure 20c). The preferential selection of generalist species at smaller scales affects the starting point of the distribution -determined by the most specialized species- but not its shape. The most specialized species have more prey at smaller than at larger spatial scales.

Network Vertical diversity

Species-Area Relationships (SARs) vary across trophic levels.

In food webs, the number of intermediate species increases faster with area than the number of top and basal species (Figure 18b). This results in steeper slopes of SARs for intermediate species. Networks where top predators are heavily specialized, i.e., host-parasitoid networks, should be an exception, with steeper slopes as trophic level increases.

The proportion of omnivorous links increases with area promoting an increase of food chain length.

The faster increase in the number of intermediate species with area facilitates the growth of the number of links among intermediate species (e.g., intraguild predation) generating an increase of food chain length.

Network Modules

Network modularity is constant across spatial scales in homogeneous landscapes.

Heterogeneous landscapes, however, are likely to promote the emergence of network compartments due to, for example, the effect of species sorting. This will likely generate an increase of modularity with area, as more compartments will be captured as the area sampled increases.

2.4.2 Beyond single trophic levels: multi-trophic SARs and NARs

The spatial scaling of network structure cannot be fully explained by the increase in species richness with area. It is well established that species richness affects several food web properties. In many cases, differences in network properties simply result from differences in species richness between the communities studied [99]–[102]. However, the spatial scaling of species richness is likely to vary across trophic levels [88], [95], [96]. This differential scaling has further consequences for the variation of trophic network structure with area [88], [96], [98]. Recently, Roslin and colleagues [96] showed that the slope of the species-area relationship steepens from plants to herbivores and from primary to secondary parasitoids. This in turn triggers a decrease in food chain length from large to small islands. In contrast, our *Trophic Sampling* model showed the steepest species-area slope for intermediate species (Figure 18b). This contrasting result can be attributed to the fact that parasitoids tend to have exceptionally narrow diet breadths when compared with other top predators, being classified as a separate category within food webs in comparative analyses [184]. We considered wider diet breadths for top predators,

which allowed them to overcome the trophic constraint [88], [95], and therefore, reduce the slope of their SARs by being selected locally even when the number of species was small. The *Trophic Sampling* model thus shows that, in the absence of spatial structure, and in totally homogeneous communities, different SARs across trophic levels will emerge and will bias NARs towards higher fractions of intermediate species and longer food chains.

In the theoretical work developed by Brose and colleagues [109], where they derived the spatial scaling of trophic links with area by combining the species–area relationship and the link–species relationship, they predicted the effect of having different SARs across trophic levels for the scaling of the number of links with area. Here we extended the analyses of this effect to many other aspects of network structure beyond the number of links (e.g. degree distributions, mean food chain length or modularity). By using a mechanistic approach to understand the spatial scaling of network structure we can determine the specific effects of each process tested and generate specific and testable predictions on how network structure will change with area depending on the spatial scenario and the processes in operation.

In agreement with our expectations, the *TTIB* model exhibited a strong variation of network structure with area, mediated by the preferential selection of generalist species that emerges from the trophic constraint (Figure 20). The effect of this constraint on species occupancy decreases with area because the total number of species increases, whereby the chances of finding a suitable prey also increase. Thus, colonisation-extinction dynamics favoured greater occupancy of generalist consumers in small areas, where fewer prey are available. The occupancy for a given colonisation and extinction rate is predicted to reach an asymptote with increasing prey species richness, because for larger diet breadths, consumers are no longer constrained to find their prey [86], [186]. The comparison between the *TTIB* and its non-constrained *TIB* version, shows a faster initial increase in complexity (i.e., species and links/species) for communities assembled using the *TIB* with a levelling off for larger areas, illustrating the loss of importance of the trophic constraint as area increases (Supplementary Figure 2.7). Therefore, as the area sampled increases, the proportion of specialist species also increases (Figure 20a-b).

Food web degree distributions are usually skewed (many specialists, few generalists) [6], [18], [190]. In spite of the fact that smaller islands host species with larger potential diet breadth (i.e., species indegree in the metaweb; Figure 20a-b), the indegree distributions of the realized food webs kept this characteristic skewness (Figure 20c). Given the importance of the degree distribution to community robustness to species loss, this suggests that food web robustness is preserved across spatial scales. The *TTIB* thus suggests that important features of network structure might reflect those present in the regional

pool and are maintained across spatial scales, as it is shown for the degree distribution.

2.4.3 Dispersal in multi-trophic metacommunities and NARs relationships

Dispersal is a key process driving species-area relationships [80], [191], [192]. Competitive meta-community models, for instance, have shown that moderate to intermediate levels of dispersal reduce local competitive exclusion, increasing local diversity via colonization-competition trade-offs [192]–[195] or by enhancing source-sink dynamics when resources are heterogeneously distributed in space [191], [196]. However, high levels of dispersal would homogenize local communities, leading to regional competitive exclusion and to reductions of the overall diversity [191], [197].

The *Trophic Meta-community* model also predicts that local diversity increases with dispersal, reducing differences between patches (i.e., lower beta-diversity) and leading to a more homogeneous meta-community (Supplementary Figure 2.4). The higher the dispersal rate, and thus the lower spatial beta-diversity, the smaller the effect of increasing area on network properties because sampling a small number of local communities is enough to capture the structure and composition of the regional community (Supplementary Figure 2.5). However, given the absence of direct competitive interactions in our models, both regional and local diversity will increase until they reach the maximum number of species in the regional pool. This observation may differ in presence of top-down regulation. Our models used a bottom-up sequential food web assembly, with the food chain consistently increasing with the addition of new species. Future explorations of the effect of dispersal on the structure and composition of multi-trophic communities should integrate the trophic constraints used here together with indirect competitive interactions.

Pillai and colleagues [110] used a meta-community model to explain the emergence of complex food webs through the linkages between patches provided by omnivorous and generalist species. In our models, consumer's diet specialization constrains the probability of finding a required resource, and hence, disfavour the presence of specialist consumers in local communities. Given that generalist and omnivorous consumers have more potential resources, they are more likely to persist, which allows for the emergence of network complexity (i.e. higher species richness with more links and links per species) in space when local patches are aggregated. Yet, the role of generalists for the spatial scaling of network complexity depends on dispersal. Under dispersal limitation, where a lower number of species coexist locally, generalists are key for the spatial scaling of food web complexity because they are the ones spatially connecting patches. However, in the absence of dispersal limitation, a higher number of species coexist in local communities, increasing the probability of specialists encountering their required prey,

and thus, generalists are no longer key contributors to the increase of food web complexity in space. This increase in complexity enhanced by dispersal, at both local and regional scales, might have important implications for the study of the stabilising effect of space on ecological communities [122], [182], [198].

2.4.4 On the need to incorporate the spatial scale in comparative network studies

Empirical characterizations of species interaction networks often fail to acknowledge the spatial scale at which these networks are observed. The restricted number of empirical studies that have done so support our theoretical predictions for several network-area relationships. The variation in food-chain length with ecosystem size (e.g., lake volume) is an example. Although ecosystem productivity can modulate this variation [62], ecosystem size on its own is a good predictor of food-chain length [199]. Our models agree with this empirical observation, showing that mean food chain length increases with area.

Our predictions of NARs suggest caution must be exercised in comparative studies of network properties. If network properties vary systematically across spatial scales, then comparative network studies that fail to acknowledge the spatial scale at which the study was performed will wrongly estimate the causes of variation of the structure of ecological networks.

The variability observed in food web properties often disappears when species richness is controlled for [99]–[102]. Then, as area also affects species richness, a key question is to what extent comparative studies addressing variation in network properties need to control additionally for the area sampled, or if the effects of area on network properties are solely driven by richness. In our models, area not only determines the number of species but also their identity based on their feeding traits (i.e., more or less generalists) and where they are placed within the food web (i.e., across trophic levels). Regardless of area, for a given number of species, we observe differences across models in terms of other network properties (Figure 21b-c), suggesting that each spatial process has different effects on structuring communities. While network complexity metrics are highly correlated with species (i.e., for a given S , there is no variation across models), vertical diversity properties are not fully explained by the number of species. For instance, network mean indegree (i.e. mean generality) (Figure 21b) shows little variation between models once controlled by the number of species; and this variation disappears when we additionally control by connectance [103]. However, the proportion of species at each trophic level (Figure 21c) is difficult to predict solely from the number of species, given that each spatial process affects these proportions differently. This suggests that controlling for both species richness and connectance will account for most of the variation in complexity properties across spatial scales, and hence it would suffice in comparative studies, but it would not explain all the variation observed in vertical diversity properties.

Therefore, incorporating the spatial scale of sampling in comparative studies would provide additional key information on the scaling of certain network properties.

Moreover, we cannot disregard the effects of habitat size in more complex environments. Our models and the few empirical NARs available mostly concern communities from relatively homogeneous environments. In more heterogeneous landscapes, other processes are at work, such as species sorting (i.e., species have different preferences for different habitats within a given area) and priority effects. Intense species sorting would likely create compartments and result in modular or compartmented webs [200], [201]. Food webs are compartmented when interactions between species are either more numerous or stronger within the compartment and few or weak between compartments [200], [201]. Our results show very little variation on the modular structure of the communities across spatial scales, but this prediction is likely to be affected when environmental heterogeneity is considered, revealing a potential effect of area on network properties independent of species richness and connectance.

2.4.5 Implications for conservation

Habitat destruction is the primary cause of the erosion of biodiversity [202]–[204]. SARs have been extensively used to estimate species loss due to habitat loss [178]–[180]. Understanding its effects on the structure of ecological networks is crucial to better preserve ecosystem structure and functioning [205]–[209]. Our results provide insights into how habitat loss and fragmentation would lead to network simplification, reducing not only species richness, but also, and perhaps more importantly, their interactions. Nonetheless it is important to distinguish the effect of losing habitat (i.e., moving across the x -axis in Figures 19 and 21a) from the effect of limiting species dispersal (i.e., different dispersal scenarios in Figure 21a and Supplementary Figure 2.5) by, for example, habitat fragmentation. Our results suggest that habitat loss should reduce the number of links per species (L/S), the proportion of omnivorous species, and shorten food chains (MFCL). Additionally, we observe that fragmented communities with higher dispersal limitation should be less complex across spatial scales, with e.g. less species and less links per species. In general, our framework shows that fragmented communities should be expected to be less resistant to habitat loss showing dramatic changes in food web structure even for small habitat reductions (Figure 21a and Supplementary Figure 2.5).

2.4.6 Limitations and future research

Species interactions can experience spatial turnover by themselves, correlated or uncorrelated with species composition turnover [135]. Even if two species co-occur in space, they may not interact if the environment is not favourable enough [210], if one of them is rare [211], or if they experienced

phenological mismatches [137]. Also, we have assumed dispersal constancy across trophic levels. Different scales of movement across trophic levels [120], [182], may also promote variation in network structure across space. Incorporating such processes into theoretical frameworks like the one presented here could increase the accuracy of our predictions.

Despite the realization that the effect of area on network properties is intimately related to that of richness or connectance, NARs open new possibilities to explore network stability and functioning across spatial scales. Several aspects of food web structure and complexity have been studied locally and related to community stability and functioning, such as the importance of diversity [212], the presence of stabilising modules like the omnivorous loop structures [213], [214] or the predominance of weak interactions [215], [216]. Scaling up in space alters network properties suggesting that community stability and functioning might also vary across spatial scales. Assessing network structure at different spatial scales can, therefore, provide new insights to analyse and understand community stability and functioning in relation to the different processes that are at play at each spatial scale.

Acknowledgements:

We warmly thank Jean-Francois Arnoldi, Matthieu Barbier and Bart Haegeman for numerous discussions and critical reading of preliminary drafts, that improved the quality of this paper. This work was funded in part through the French Laboratory of Excellence Project 'TULIP' (ANR-10-LABX-41; ANR-11-IDEX-002-02), by a Region Midi-Pyrénées Project (CNRS 121090), by a grant from the Canadian Institute of Ecology and Evolution, and by the NEWFORESTS project.

Author contributions:

NG, DG, BC and JMM designed research. NG, ML, DG and JMM conducted research and contributed to the model. NG, DG and JMM wrote the paper and all authors contributed to the edition and discussion.

SUPPLEMENTARY MATERIAL CHAPTER 2

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Supplementary Methods

We explore the effect of each process on the spatial scaling of food web structure with three models of multi-trophic community assembly. They all consider the same regional food webs (or metawebs) from which species are selected to conform local communities, and the local assembly processes of the three models follows the same trophic constraint, i.e. consumers need to have at least one resource in the local community. In addition, we have a non-trophic constrained version of each of the models presented below. Supplementary Figure 2.7 provides the comparison between the two versions, which shows that most of the differences occur at small areas where the effect of the trophic constraint is stronger. We then analysed several network properties at different spatial scales, which allowed us to characterize a suite of NARs. In this section, we first explain how we generated the regional food webs, we then present each community assembly model, and we finally explain the network properties analysed, the beta-diversity metrics used, and the statistical analyses conducted.

Regional food webs (Metawebs)

We used the niche model (Williams & Martinez 2000) to generate food webs that were used as the regional pool of species for the three models. The niche model requires two input parameters: the number of species (S), and network connectance (C) defined as the fraction of realised links among the possible links (i.e. $C=L/S^2$). This model describes trophic niche occupancy between consumers and resources along a resource axis. It generates model food webs that approximate well the central tendencies and the variability of a number of empirical food web properties (Williams & Martinez 2000; Dunne et al. 2002; Stouffer et al. 2005).

We performed one hundred replicates of each of the three models using that same number of distinct regional food webs generated using the niche model with $S = 200$ and $C = 0.056$ as input parameters. The stochastic nature of the niche model ensures variability across the replicate networks. The value for C was assigned following the power decay of C as S increases found in empirical networks ($C = \sigma S^{-\lambda}$, where $\sigma = 0.8$ and $\lambda = 0.5$; Cohen & Briand 1984; Montoya & Solé 2003; Ings et al. 2009). The specific values of S and C , however, did not affect qualitatively our results (See Supplementary Figure 2.8). For a full description of the regional network (or metaweb) properties see Supplementary Table 2.1.

Local food web assembly models

a) *Trophic Sampling model*

This model randomly samples networks of different sizes from the 200-species regional food web (i.e., the metaweb) described above. This is not a spatial model, and as such there are no occupancy dynamics (i.e., there are no spatial processes involved in the local community assembly process) (Box 1). The assembly process was exclusively constrained by the requirement that each consumer species needed to have at least one prey in the local community. Thus, for each area we randomly selected samples from the regional food web with the number of species required and we checked that all selected consumers have at least one prey. If the trophic requirement was not satisfied, the subsample selected was excluded from the analyses. To obtain the number of species for a given area, we used $S = kA^z$, with $k = 10$ and $z = 0.27$. Therefore, to sample different number of species we generated a range of area sizes that covers the entire spectrum of species available in the pool. The value of z used ($z = 0.27$) was derived from a meta-analysis performed by Drakare *et al.* (2006), which is widely regarded as the best empirical estimate for terrestrial systems. The value of k corresponds to the smallest local community. We used the power function since it is one of the best known and most common reported relationships in the literature (Arrhenius 1921; Tjørve 2003; Scheiner 2003). The power law has been shown to be the central phase of a triphasic curve: SAR is concave at local scales, approximately linear at regional scales, and finally convex at continental scales (Rosindell & Cornell 2007). Therefore, the mechanisms, expectations, and results presented in our theory would reflect local-to-regional scale dynamics.

The *Trophic Sampling model* can be considered as a baseline reference for NARs, where the increase of species richness with area is constrained by the simplest food web assembly process: the occurrence of a predator is mediated by the presence of one of its prey. Even though the processes tested with this model (i.e., link-area scaling and SARs dependency on trophic level) are not exclusive of this assembly process, we are interested in the patterns emerging from the model with the simplest assumptions.

b) *Trophic Theory of Island Biogeography model*

The trophic theory of island biogeography (*TTIB*; Gravel *et al.* 2011) predicts the structure of food webs on islands connected through immigration to a mainland, which in turn contains a large regional species pool. The structure of the local assembly of species and their interactions is defined by the equilibrium between colonisation and extinction dynamics. It considers the additional constraint of consumers requiring at least one prey on the island to colonize and persist. The ratio between colonisation and extinction (for a fixed colonisation rate) is considered a proxy of geographical area; the smaller the

ratio the smaller the area (MacArthur & Wilson 1967; Gravel et al. 2011).

In this model, we assumed species from the regional metaweb could colonise the island with a fixed colonisation probability ($c=0.2$) and could go extinct with an increasing extinction probability ($e = \{0.01, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5\}$). These parameter values allowed the exploration of a range of local communities that correspond to islands of different area (i.e., area size in this model is given by the c/e ratio). For each combination of parameters (extinction, colonisation) and for each of our regional networks, we ran simulations for a total of 1000 time steps, which is enough to reach the equilibrium between colonisation and extinction dynamics and, therefore, to determine the number of species for a given island (see Gravel et al. 2011 for details). This is a discrete time one-patch species occupancy model, in which the occupancies of all species are determined by the trade-off between c and e plus prey availability. To calculate the final species configuration for a given combination of c and e , in each time step of the simulation we sequentially went over each species in the network and stochastically determine its extinction or colonisation based on the corresponding rates and whether there are resources present for that species. Secondary extinctions were calculated after primary extinctions occurred. We checked for all species that lost their resources and repeated this check until no further extinctions were found. Network properties were computed for resulting networks at the end of the simulation (i.e., time step 1000).

The difference between this *TTIB* model and the *Trophic Sampling* model lays on the complexity of the assembly process. The stochastic nature of the community assembly enforced by the *TTIB* model, which is the result of colonisation-extinction dynamics, favours the persistence over time of generalist consumers. Specialist consumers that depend on a single resource are more prone to become secondarily extinct given the trophic constraint: if their only resource goes stochastically extinct, they go extinct too. In contrast, the *Trophic Sampling* model only searches for possible configurations of a given number of species where every consumer needs to have a resource, without subjecting the selected community to additional stochastic extinctions.

c) *Trophic Meta-community model*

We used a multi-trophic meta-community model (Box 1) to determine the effects of spatial variability in species distribution (i.e., beta-diversity) on NARs. We used different levels of dispersal among local communities to generate beta-diversity in space. Seventy-five local communities (patches) were randomly placed on a 2-dimensional Euclidean space of 1 unit of length on each dimension and the distances between patches were calculated. Patch pairs were considered to be connected if the distance between

them was less than or equal to 0.3, because it provided a good balance between local species richness and spatial heterogeneity in species composition. Connections between patches were the same for all species and were bidirectional and homogeneous, i.e., dispersal probabilities were equal across every pair of connected patches, and there was no dispersal between non-spatially connected patches. A different (randomly generated) network of patches was used for each replicate.

We used the same regional networks as in the previous models. At each time step, species could arrive to each patch from the regional pool independently of each other given a fixed colonisation probability ($c = 0.1$) and could go locally extinct with a fixed probability ($e = 0.4$). We chose these values for c and e because they allowed for a local community size that yielded a good trade-off between species richness at the local and regional scales.

Additionally, at each time step all species present in a given patch could disperse to a connected patch according to a given dispersal rate. We ran two versions of this model using two different values for the dispersal rate $d = \{0.01, 0.1\}$. This allowed us to test the effect of different levels of dispersal on the spatial scaling of network structure. Within each version of the model, dispersal rates were constant across all species. As for the *TTIB* model, stochastic colonisation-extinction dynamics were dependent on the trophic constraint (i.e., on the availability of resources for each consumer present). Similarly, dispersal followed the same trophic constraint. That is, consumers could only disperse to those connected patches where there was at least one of their resources. Simulations were run for 1000 time steps to achieve an equilibrium state in terms of species composition. Similarly to the *TTIB*, this is a discrete time patch occupancy model, only this time it is multi-patch. At each time step, extinction, colonisation, and dispersal dynamics are calculated sequentially for every patch and species. Occupancy time series were thus created by calculating extinction and colonisation independently at each local patch and then calculating the dispersal probabilities across neighbouring patches. Network properties were again analysed (as for the *TTIB*) over the food web resulting at the end of the simulation.

The spatial scale was determined by the spatial aggregation of several local communities in an ever-increasing way from 1 (a single local community) to 75 (maximum number of communities; the regional scale). That is, the largest spatial scale was the complete aggregation of all local communities, which yielded the total set of species of the regional species pool if every species persisted at the regional scale after the simulation. The aggregation procedure was based on neighbouring aggregation, whereby local communities were aggregated based on the distance to their neighbours. One local community was selected randomly as the starting point. This process was repeated 75 times selecting every local

community as a different starting point. It is important to notice that in this model communities were assembled at the local scale (i.e., in each local patch) while the spatial scale of sampling increased with the aggregation of different local patches. Therefore, the spatial scale of sampling differs from the scale at which the assembly takes place. In contrast, in the two previous models the scale of sampling is the scale at which the assembly process occurs. This difference is key to understand the components of the spatial scale that each model captures. While the *Trophic Sampling* and the TTIB consider ‘complete’ areas (i.e., area = island area), the *meta-community* model considers a sub-area of a larger region. Therefore, while the first two models capture the effect of alpha diversity, the latter also captures the effect of beta-diversity. After the generation of different food webs for each of the three models, the corresponding area was rescaled to fall in the range between 0 and 1, where 0 is the smallest local scale and 1 is the largest regional scale, to allow model comparison.

Network properties

We classified NARs into three categories: vertical diversity, complexity, and modules.

Vertical diversity properties included the fraction of omnivory (fraction of species feeding from more than one trophic level; O), mean food chain length (mean number of links needed to get from the basal species to the top species, restricted to a bottom-top direction, with paths from more than 1 basal species being averaged; $MFCL$), fraction of basal species (species without prey; B), fraction of intermediate species (species with predators and prey; I) and fraction of top species (species with predators; T). Notice that the fraction of intermediate species includes both primary and secondary consumers. For consistency with the literature on food web research, we keep the analysis on the fraction of intermediate species as a whole. However, we also analyse individually primary consumers, secondary consumers and omnivorous species that form the intermediate trophic level.

Network complexity properties included the number of species (S), number of links (L), connectance ($C=L/S^2$), links per species (L/S), mean indegree (average number of prey items per predator; also known as mean generality) and mean outdegree (average number of predators per prey species; also known as mean vulnerability).

Module properties included network modularity (M), which indicates the presence of densely linked groups within a network (Newman & Girvan 2003), and three-species trophic motifs as building blocks of complex networks (Milo et al. 2002; Bascompte & Melian 2005; Camacho et al. 2007). The trophic motifs have been used as an indication of the modules that are structurally over- or under-represented in food webs. We calculated the proportion of (i) tri-trophic food chains, (ii) apparent competition, and (iii)

exploitative competition motifs across spatial scales.

Additionally, to assess the extent to which more generalist consumers are better colonisers in smaller areas, we calculated the distribution of the diet breadth of those consumers present in a given patch. To do so, we considered their potential diet breadth (i.e., indegree or generality), defined as the number of resource species they consume within the regional metaweb. We call this the *potential indegree distribution*. Additionally, we calculated the *realized indegree distribution* within each island. This property reflects the consequences of the preferential selection of generalist consumers on the structure of the realized local network. For the realized indegree distributions, we calculated the cumulative probability at each spatial scale $P_c(k)$, for $\geq k$, where $P_c(k)$ is the probability a species has k or less prey in the network.

Beta-diversity metrics

In order to assess the level of dissimilarity on species composition among local communities (i.e., species *beta-diversity*) depending on the level of dispersal, we used the metrics developed by Baselga et al., (2017), available in ‘betapart’ package in R.

For accounting for the total beta-diversity we used the multiple-site Sorensen index:

$$\beta_{\text{SOR}} = \frac{[\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_{i<j} \max(b_{ij}, b_{ji})]}{2[\sum_i S_i - S_T] + [\sum_{i<j} \min(b_{ij}, b_{ji})] + [\sum_{i<j} \max(b_{ij}, b_{ji})]}$$

where S_i is the total number of species in site i , S_T is the total number of species in all sites considered together and b_{ij} , b_{ji} are the number of species exclusive to sites i and j , respectively, when compared by pairs.

Additionally, we calculated the turnover of interactions computing the number of interactions in common between two local communities instead of the number of species. In our models, interactions turnover is determined by the absence of one or the two interacting species (i.e. species beta-diversity) because interactions are determined by the metaweb. That is, if two species co-occur locally and they have a link in the metaweb they will always interact locally. No differences were observed when comparing the patterns for species turnover and interactions turnover.

Statistical analyses

Mean and standard error of the mean among the 100 replicates of each of the simulation experiments were calculated for each food web property and plotted using generalised additive models (GAM) with the R package 'ggplot2' (Wickham 2009). GLMs were used to analyse differences in SARs depending on species trophic level and to analyse the variation of the number of links with species richness for the *Trophic Sampling* model.

We fitted bounded exponential curves ($f(x) = L(1 - he^{-gx})$; where L represents the curve's maximum value, g the steepness of the curve and h determines the fraction of L where the curve starts) using nonlinear least squares (NLS) with the 'nls' function in R. Growth exponents were used to quantify the rate of growth of network properties with area.

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Supplementary Table 2.1. Description of the metawebs used in the theoretical models. A 100 different metawebs were used.

Property	Mean(Standard deviation)
Number of Species	200(0)
Connectance	0.056(0.004)
Number of links	2209.3(160.9)
Links per species	11.04(0.80)
Indegree	12.48(0.88)
Outdegree	11.63(0.99)
Mean food chain length	12.26(1.08)
Proportion of basal	0.12(0.02)
Proportion of intermediate	0.83(0.03)
Proportion of top	0.05(0.03)
Omnivory	0.86(0.05)
Modularity	0.37(0.02)

Supplementary Table 2.2. GLM results for the differences in SAR depending on trophic level. Estimates, T values and statistical significances are indicated (***) for p-values<0.001; ** for p-values<0.01; * for p-values<0.05) for the slope and intercepts of the relationships. Basal was set as reference level, that is, values for Intermediate and Top show the deviation from Basal values.

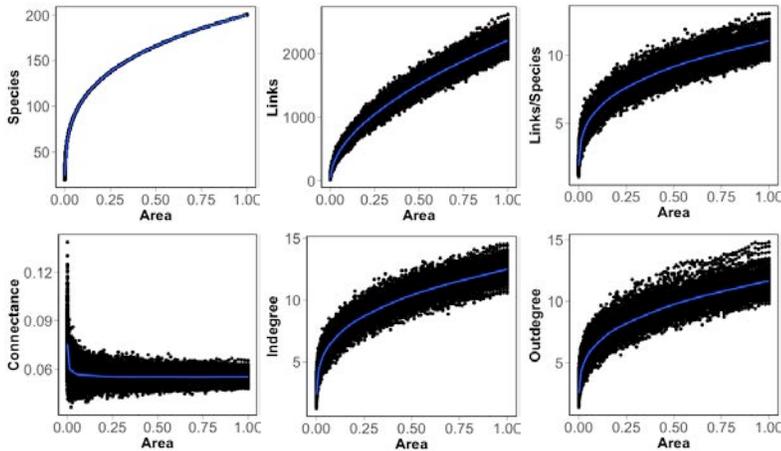
		Estimate	T value
Basal	Intercept	1.38	605.98 ***
	Slope	0.10	72.55 ***
Intermediate	Intercept	0.84	262.19 ***
	Slope	0.23	112.16 ***
Top	Intercept	-0.48	-149.55 ***
	Slope	-0.03	-17.07 ***

Supplementary Table 2.3. Fit of each network property of each model to a bounded exponential function ($f(x) = L(1 - he^{-gx})$), where L represents the curve's maximum value, g the steepness of the curve and h determines the fraction of L where the curve starts. We used nonlinear least squares (NLS) with the 'nls' function in R.

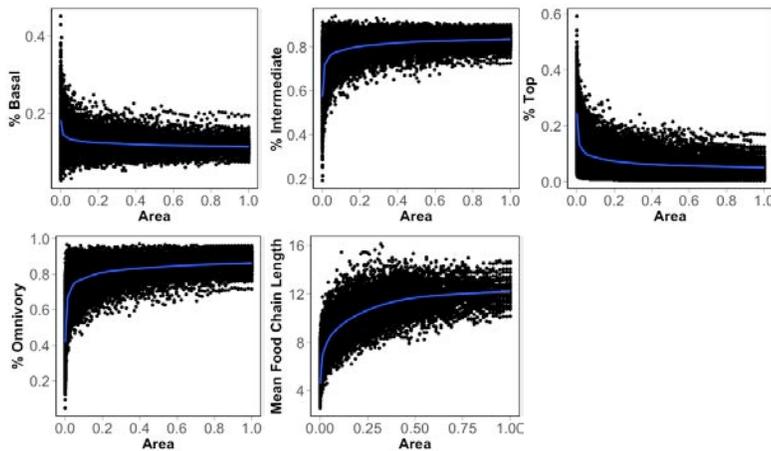
Network property	Model	t value			Estimate		
		L	g	h	L	g	h
Species	Trophic Sampling	918.9	219.2	1043.2	183.2	5.13	0.75
	TTIB	358.50	79.42	397.80	181.2	10.7	0.95
	Dispersal 0.01	1020.2	136.6	260.1	173.8	6.5	0.78
	Dispersal 0.1	2897.9	89.95	162.82	193.7	34.2	0.41
Links	Trophic Sampling	359.9	169.6	1821.3	2350	2.1	0.93
	TTIB	250.04	67.18	412.37	1925	5.8	1
	Dispersal 0.01	461.76	88.45	182.21	1842	5.2	0.95
	Dispersal 0.1	996.27	44.37	80.33	2108	34.1	0.6
Links/species	Trophic Sampling	602.3	143.6	702.4	10.19	4.82	0.72
	TTIB	240.44	49.63	240.17	10.06	12.3	0.86
	Dispersal 0.01	788.49	79.78	139.45	10.30	9.5	0.74
	Dispersal 0.1	1129.01	23.06	50.38	10.86	69.9	0.37
Connectance	Trophic Sampling	1002.65	27.72	-62.63	0.055	558.8	-0.30
	TTIB	63.577	8.524	-18.49	0.057	58.3	-0.62
	Dispersal 0.01	629.03	38.06	-68.66	0.060	7.9	-0.39
	Dispersal 0.1	987.55	15.08	-25.44	0.056	15.7	-0.15
Indegree	Trophic Sampling	616.1	130.8	609.8	11.57	5.05	0.66
	TTIB	245.31	47.92	232.22	11.43	11.85	0.81
	Dispersal 0.01	851.01	74.91	128.24	11.87	11.6	0.72
	Dispersal 0.1	1174.37	20.55	49.15	12.33	85.7	0.35
Outdegree	Trophic Sampling	554.1	126.7	609.6	10.75	4.89	0.70
	TTIB	215.38	40.95	97.23	10.70	12.03	0.79
	Dispersal 0.01	683.20	66.31	116.24	10.91	9.39	0.70
	Dispersal 0.1	968.08	18.74	40.71	11.45	68.9	0.34
MFCL	Trophic Sampling	570.71	89.41	346.62	11.37	10.15	0.57
	TTIB	170.33	31.17	136.32	11.57	18.91	0.72
	Dispersal 0.01	592.62	49.65	88.41	11.53	9.93	0.53
	Dispersal 0.1	657.603	9.904	25.29	12.01	82.16	0.23
% Basal	Trophic Sampling	272.61	68.35	-134.8	0.14	25.7	-1.35
	TTIB	41.75	10.93	-20.12	0.12	42.69	-1.19
	Dispersal 0.01	246.28	39.01	-73.75	0.13	5.87	-0.85
	Dispersal 0.1	407.72	11.20	-18.91	0.11	13.36	-0.24
% Intermediate	Trophic Sampling	1061.69	70.92	218.02	0.78	30.5	0.37
	TTIB	160.61	22.07	62.11	0.80	67.46	0.64
	Dispersal 0.01	1143.57	39.52	67.72	0.80	12.16	0.28
	Dispersal 0.1	1711.599	9.424	16.655	0.82	29.61	0.07
% Top	Trophic Sampling	121.40	30.38	-60.53	0.066	44.22	-1.56
	TTIB	16.90	12.62	-12.85	0.065	46.96	-3.4
	Dispersal 0.01	110.17	21.74	37.67	0.05	42.84	-2.94
	Dispersal 0.1	126.538	3.149	-9.380	0.05	122.9	-0.64
% Omnivory	Trophic Sampling	908.34	62.52	179.81	0.81	67.64	0.47
	TTIB	152.92	24.95	74.05	0.82	56.45	0.75
	Dispersal 0.01	1042.21	36.27	64.94	0.84	31.67	0.45
	Dispersal 0.1	1403.842	7.065	16.186	0.85	78.74	0.09

Supplementary Figure 2.1. Network-Area relationships (NAR) for the Trophic Sampling model. Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. Properties giving information about food web a) complexity, b) vertical diversity and c) motifs and modularity. Notice that the Species-Area relationship shown in (a) is given by $S = kA^z$, with $k = 10$ and $z = 0.27$. Simple representations of network motifs are shown in the corresponding panels; Nodes represent species and arrows trophic interactions from prey to predators.

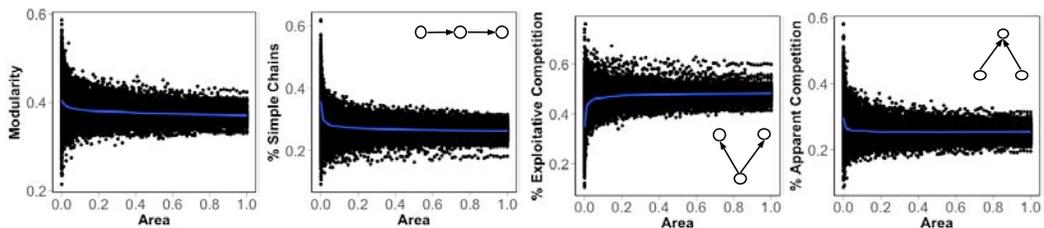
a) Complexity



b) Vertical diversity

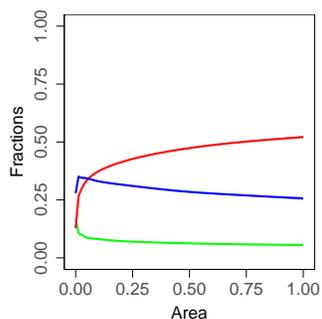


c) Motifs and modularity

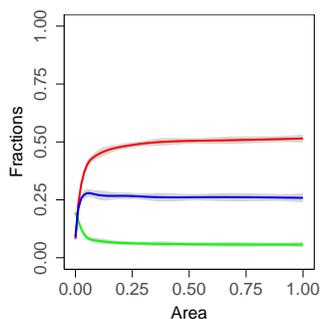


Supplementary Figure 2.2. Decomposition of the intermediate trophic level. Relationship of the fraction of species of each group with area for (a) the *Trophic Sampling* model, (b) the *Trophic Theory of Island Biogeography* model, (c) the *Trophic meta-community* model with low dispersal ($d=0.01$) and (d) high dispersal ($d=0.1$). Green: herbivores species (i.e. species only consuming basal species); Blue: carnivores (i.e. species only preying on other consumer species); Red: omnivorous species (i.e. species consuming both basal and consumer species). It is important to notice that all these groups only refer to those species included in the intermediate trophic level, it does not consider top species.

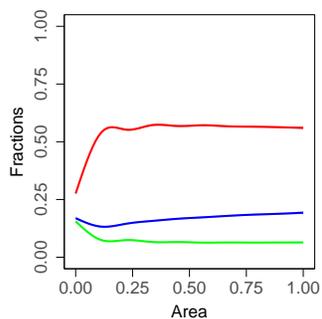
a) Trophic Sampling



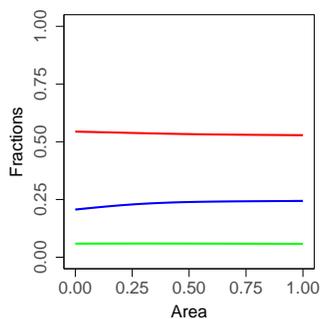
b) Trophic Theory of Island Biogeography



c) Trophic Metacommunity Low dispersal

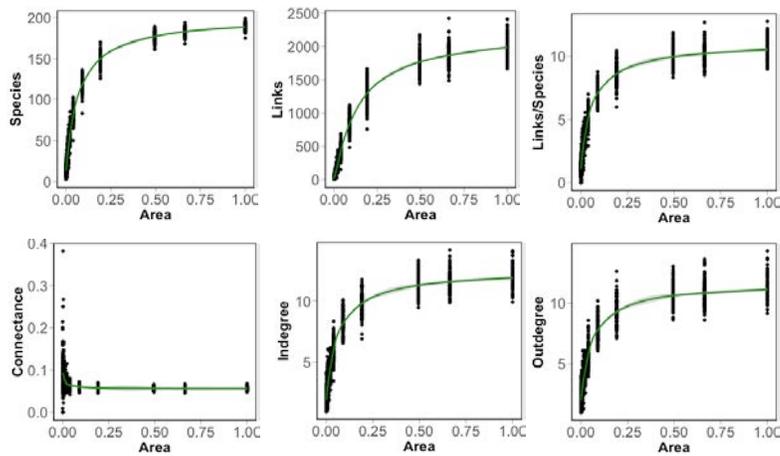


d) Trophic Metacommunity high dispersal

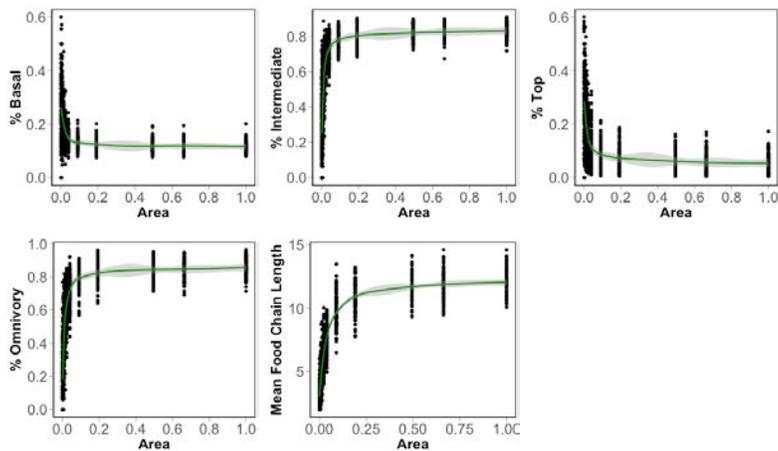


Supplementary Figure 2.3. Network-Area relationships (NAR) for the TTIB model. Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. Properties giving information about food web a) complexity, b) vertical diversity and c) motifs and modularity. Simple representations of network motifs are shown in the corresponding panels; Nodes represent species and arrows trophic interactions from prey to predators. Shaded areas show 95% confidence intervals.

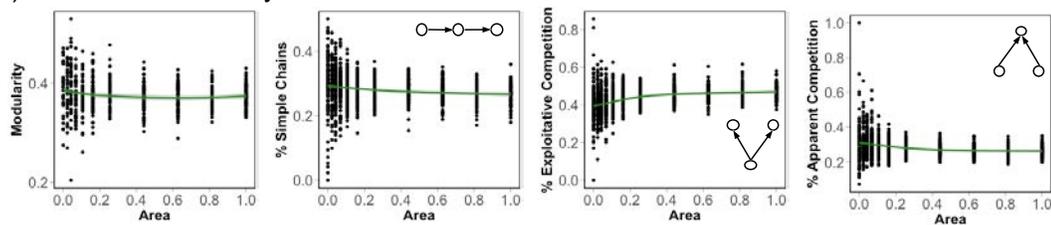
a) Complexity



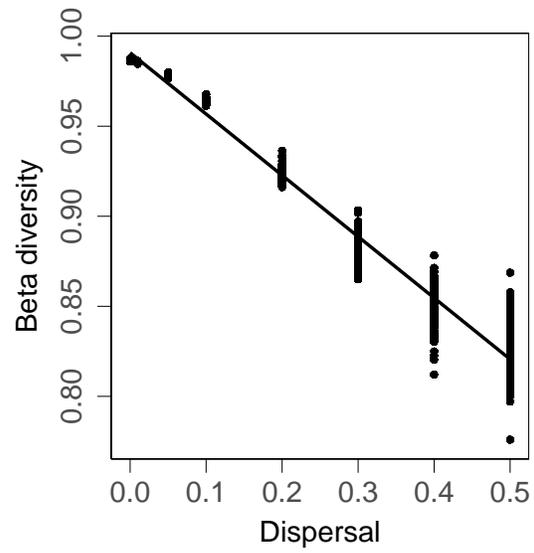
b) Vertical diversity



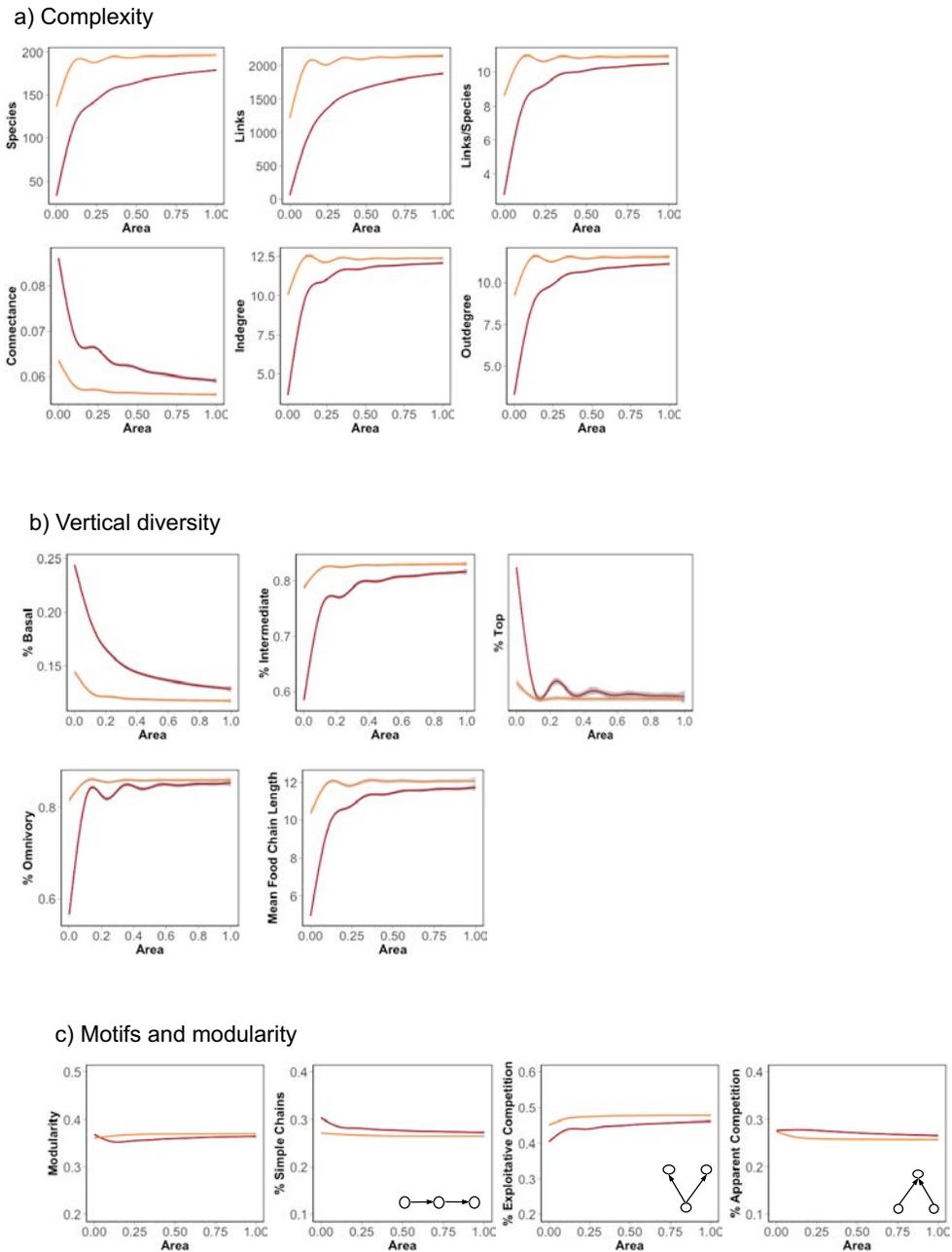
c) Motifs and modularity



Supplementary Figure 2.4. Dispersal - beta diversity relationship for the *Trophic meta-community* model. Increasing species dispersal rates increases the similarity between patches. Note that we analysed these patterns for eight different dispersal rates $d = \{0, 0.01, 0.05, 0.1, 0.2, 0.3, 0.4, 0.5\}$.

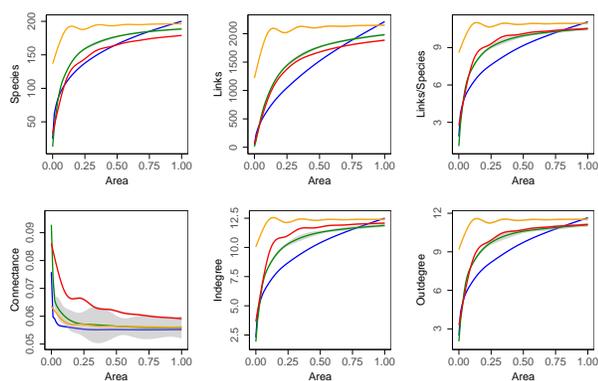


Supplementary Figure 2.5. Network-Area relationships (NAR) for the trophic meta-community model. Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. Properties giving information about food web a) complexity, b) vertical diversity and c) motifs and modularity. Red line: 0.01 dispersal rate; Orange line: 0.1 dispersal rate. Simple representations of network motifs are shown in the corresponding panels; Nodes represent species and arrows trophic interactions from prey to predators. Shaded areas show 95% confidence intervals.

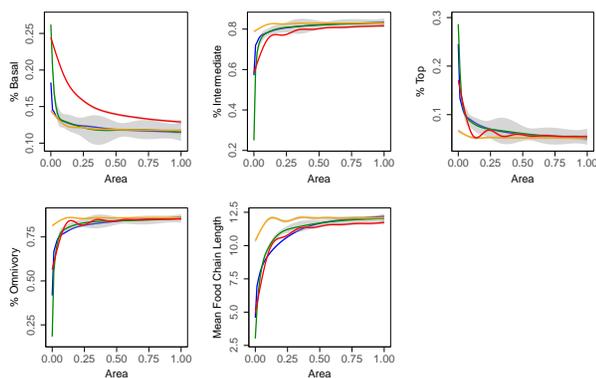


Supplementary Figure 2.6. Comparison of Network-Area relationships (NAR) across models. Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. Properties giving information about food web a) complexity, b) vertical diversity and c) motifs and modularity. Blue: *Trophic Sampling* model; Green: *Trophic Theory of Island Biogeography* model; Red: *Trophic meta-community* model with 0.01 dispersal rate; Orange: *Trophic meta-community* model with 0.1 dispersal rate. Simple representations of network motifs are shown in the corresponding panels; Nodes represent species and arrows trophic interactions from prey to predators. Shaded areas show 95% confidence intervals.

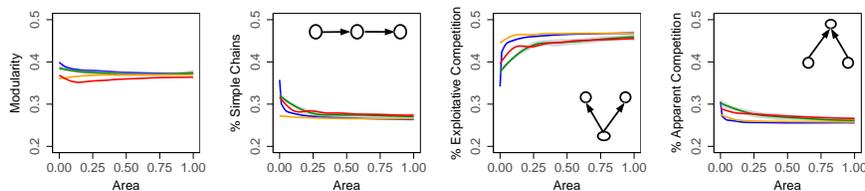
a) Complexity



b) Vertical diversity

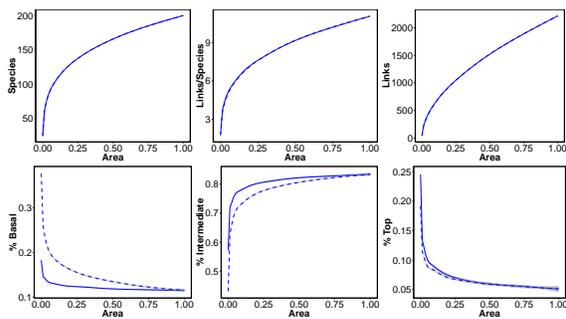


c) Motifs and modularity

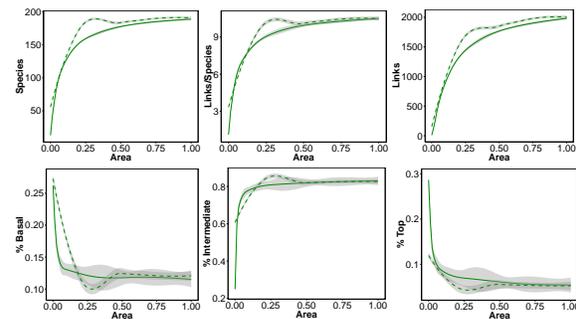


Supplementary Figure 2.7. Comparison of Network-Area relationships (NAR) for the models with trophic constraint (solid line) and without the trophic constraint (dashed line). Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. a) NARs for the *Trophic Sampling* model, b) NARs for the *Trophic Theory of Island Biogeography* model and c) NARs for the *Trophic Meta-community* model (Red line: 0.01 dispersal rate; Orange line: 0.1 dispersal rate). Notice that the non-constraint TTIB in (b) corresponds to the classic Theory of Island Biogeography model. Notice that the Species-Area relationship for the *Trophic Sampling* model shown in (a) is given by $S = kA^z$, with $k = 10$ and $z = 0.27$. Shaded areas show 95% confidence intervals.

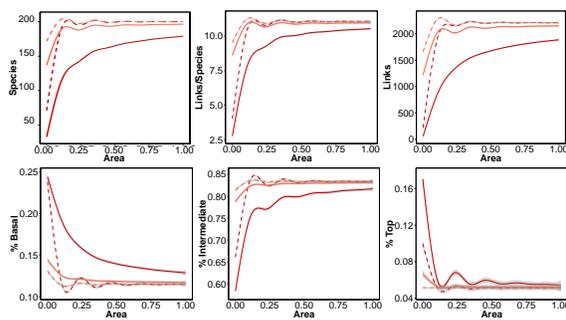
a) Trophic Sampling



b) Trophic Theory of Island Biogeography

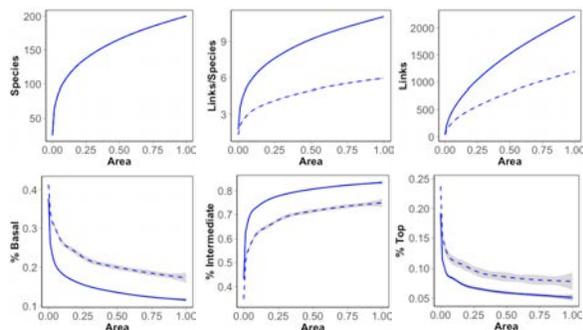


c) Trophic Metacommunity

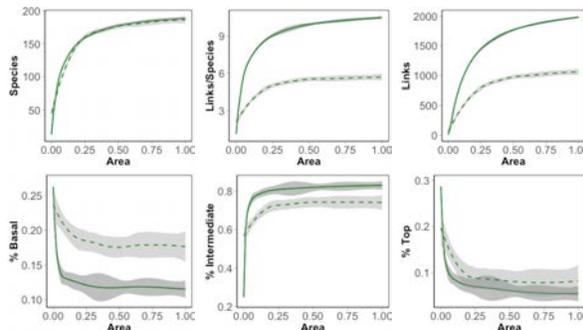


Supplementary Figure 2.8. Comparison of Network-Area relationships (NAR) for the models considering metawebs with different connectances; $C = 0.056$ (solid line) and $C = 0.03$ (dashed line). Area values close to 0 correspond to local communities and values close to 1 correspond to regional communities. a) NARs for the *Trophic Sampling* model, b) NARs for the *Trophic Theory of Island Biogeography* model and c) NARs for the *Trophic meta-community* model (Red line: 0.01 dispersal rate; Orange line: 0.1 dispersal rate). Notice that the Species-Area relationship for the *Trophic Sampling* model shown in (a) is given by $S = kA^z$, with $k = 10$ and $z = 0.27$. Shaded areas show 95% confidence intervals.

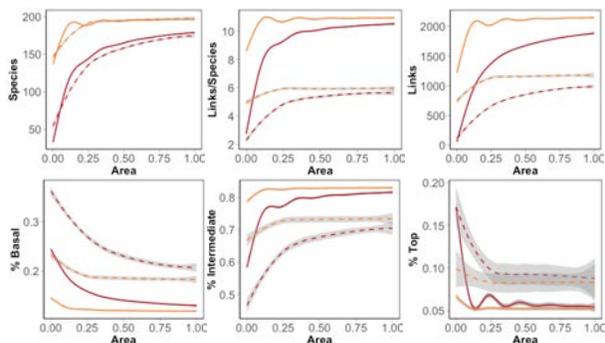
a) Trophic Sampling



b) Trophic Theory of Island Biogeography



c) Trophic Metacommunity



Chapter 3

EFFECTS OF AREA SIZE ON NETWORK STRUCTURE: EMPIRICAL APPROACH

3.1 TITLE OF THE SCIENTIFIC ARTICLE:

The spatial scaling of biotic interactions across the globe⁴

Keywords: community structure, ecological networks, spatial food webs, species-area relationship, network-area relationship, area size, islands.

ABSTRACT

The larger the geographical area sampled, the richer the ecological community. This is a pattern so universal that it has been dubbed a fundamental law of ecology. Yet, species are embedded in complex networks of biotic interactions and whether different components of network structure vary with area size, and whether they do so in a similar manner is, so far, unknown. We compiled a large set of ecological networks from different ecosystems and biomes across the globe, comprising different types of interactions (i.e., mutualistic, antagonistic) and different sampling methodologies, to analyse the universalities in the spatial scaling of network structure. We found a number of universal network-area relationships (NARs). The number of links, links per species and mean indegree (i.e., mean number of resources per consumer) increased with area size following a power law regardless of the data category or interaction type, indicating that ecological communities become more complex with area. In contrast, mean potential indegree (i.e., mean number of resources a consumer has at the regional scale) decreased across spatial scales for all data categories and interaction types, suggesting that diet specialists require larger areas to be found.

⁴ This article represents a collaboration with José M. Montoya, Miguel Lurgi, Bernat Claramunt, Marie-Josée Fortin, Shawn Leroux, Kevin McCann, Kevin Cazelles, Dominique Gravel, Tomas Roslin, Diego Vázquez, Luciano Cagnolo, Carine Emer, Wilfried Thuiller, Ingo Grass, Ingolf Steffan-Dewenter, Frank Jauker, Spencer Wood, Daniel Montoya, Jordi Bosch and Christian Mulder. In preparation.

3.2 INTRODUCTION

Research on the spatial scaling of biodiversity has traditionally focused only on the increase of species richness with area size [79]–[81]; so much so that the species-area relationship (SAR) has been identified as a universal law in ecology [81]–[83]. Yet, ecological communities are not only collections of species, but also sets of interactions between them. Ecological network research has shown the importance of biotic interactions to not only understand biodiversity organization within communities, but also to predict ecosystem responses to different components of environmental change [2], [6], [9], [46], [217], and important ecosystem functions [1], [3], [4]. Understanding how network structure change across spatial scales is, thus, fundamental to better predict ecosystem responses to perturbations and to properly interpret empirical data on ecological networks. However, research on the spatial scaling of network structure is on its infancy [103], [109], [124].

Our recent theoretical research on the spatial scaling of network structure has shown that a number of network-area relationships (NARs) can emerge from different spatial mechanisms and assembly processes (See chapter 2; [124]). Different SARs across trophic levels can generate changes in network structure as area size increases; dispersal limitation, through its effects on β -diversity, can promote changes in network structure across spatial scales, and the preferential selection of generalist species at small spatial extents generates an increase in biotic specialization with area size that can have further consequences on the structure of the network [86], [124]. As shown theoretically, there are multiple ways to build NARs and to analyse the spatial scaling of network structure, and each method of construction will reflect the role of a different ecological process [124]. The challenge is to find universal patterns across different types of systems as it has been done for the spatial scaling of species richness [94], [218].

In the SARs literature, the power function pervades the increase in species richness with area across all types of system [79], [94], [177], [219]. Yet, extensive debates still exist on the effects of the sampling schemes and methods of construction to determine the specific shape and meaning of SARs [218], [220]–[223]. Two distinct classes of data have been described based on the sampling approach used to address the patterns of species richness across spatial scales [218], [223], [224]. The first class consists of collections of sampling units which are usually aggregated to obtain larger areas. These can be of either the same size (i.e., replicates), or of increasing sizes, where smaller areas are nested into larger ones. For this type of data, species richness necessarily increases monotonically (or at least does not decrease) as the number of area units aggregated increases. The second type of data consists of independent and

isolated units of area of different sizes (e.g., islands in an archipelago, lakes or mountain tops) that can potentially result in negative species-area relationships [218], [219], [223], [224]. This differentiation has been crucial to understand the mechanisms behind the observed SARs.

Different ecological processes influencing the shape of SARs are linked to each type of data. Environmental heterogeneity, dispersal limitation or biotic interactions are well-known mechanisms underlying the shape of SARs regardless of the type of data used [94], [218]. However, there are more specific ecological processes, such as the interplay between colonization and extinction rates, that only influence the shape of SARs in data on independent units of area (e.g., islands) [80], [94], [218]. Similarly, we expect different ecological processes to also have different roles on the spatial scaling of network structure depending on the type of data considered. For example, we expect the preferential selection of generalist species in smaller areas to have a more important role in islands than in random subsamples of areas [86], [124]. Thus, understanding the variety of SARs and NARs emerging from different types of data can provide valuable information on the processes determining the spatial patterns of ecological communities, altogether revealing possible universalities. As briefly reviewed above, the influence of different types of data, and the underlying ecological processes, has been acknowledged and studied on SARs [218], [220]–[223], however, its influence for the spatial scaling of network structure remains empirically untested.

Here we compiled 35 datasets on ecological networks from different ecosystems and biomes across the globe. These comprise different types of interactions (i.e., bipartite mutualistic and antagonistic, and multi-trophic interactions) to analyse the universalities on the spatial scaling of network structure. We classified our datasets depending on the spatial structure of the data and on the spatial extent covered during the sampling of the communities and the procedure used to generate the spatial scaling. Specifically, we divided them into three categories. Replicates, which are datasets consisting on a collection of small replicated sampling units of the same size; Islands-fragments, that include datasets in which the sampling units are independent isolates of different sizes; and biogeographical data, that consists on a collection of replicated sampling units of the same size spanning large geographical gradients. For each dataset, we characterized how network structure changes across spatial scales to determine: 1) whether universal NARs exist and 2) whether there is an influence of both the type of data used (i.e., replicates, islands or biogeographical) and the type of interaction. In particular, we analysed the spatial scaling of species richness (total number and across trophic levels), number of links and links per species, consumer:resource ratio, network modularity and biotic specialization.

3.3 METHODS

We built network-area relationships (NARs) for 35 datasets comprising ecological communities of different types of interactions from different biomes across the world. This allowed us to identify universalities in the way network properties change across spatial scales for different data and interaction types. Universalities were quantified using the exponents of the relationships between all network properties analysed with area size when fitted to a power function. Here we first provide a description of the data classification, we then explain the procedure used to build NARs for each data category and we finally describe all network properties analysed and the statistical methods used to quantify the spatial scaling of the network properties and their comparison between datasets.

3.3.1 Data classification

We divided the datasets analysed into three categories (replicates, island/fragments and biogeographical) according to the spatial structure and the spatial extent covered during the community sampling (Figure 22). All datasets presented here contain information on the set of species present in a collection of localities and the ecological interactions observed between these species. Specific details about each dataset can be found in Appendix S4.1. Here we briefly describe the main characteristics of each dataset including sampling methodology and location, and interaction types considered.

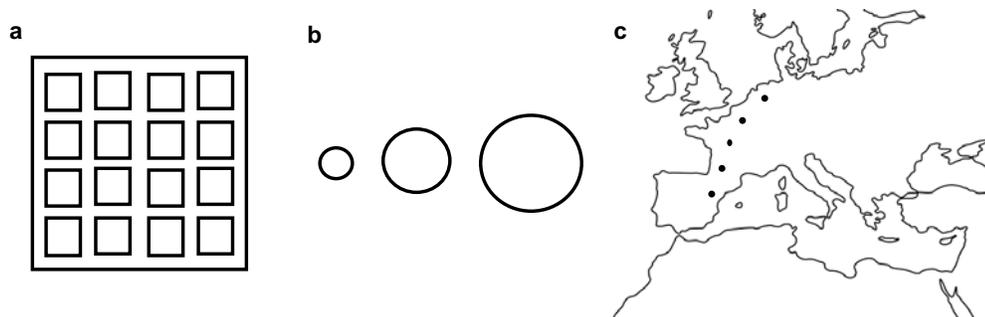


Figure 22. Data classification. We divided the datasets into three depending on the spatial structure and the spatial extent covered in each study. (a) Replicates correspond to datasets for which sampling was conducted in a small spatial extent using a collection of small replicated sampling units of the same size; (b) Islands-fragments correspond to isolated sampling units of different area sizes and (c) biogeographical data correspond to datasets with sampling units of similar sizes spanning large (i.e., biogeographical) spatial scales. Black dots represent the sampling units.

Replicates. This type of datasets comprises data for which sampling was conducted in a small spatial extent in a replicated fashion, usually using a collection of small replicated sampling units of the same size. Datasets within this category include: Host-parasitoid and plant-pollinator interactions networks from Mediterranean forests in Garraf, Montseny and Olot Natural Parks in Catalonia, Spain; host-parasite interactions involving insect herbivores of the Pedunculate Oak (*Quercus robur*) and their parasites in a temperate forest in Sweden; plant-pollinator interactions from a grassland environment in the Argentinian Patagonia; soil food webs from farmlands across Germany; terrestrial food webs within small islands of similar sizes of a temperate saltmarsh mudflat in southern UK; and intertidal food webs comprising marine invertebrates from Northwestern North America.

Islands-Fragments. This category included datasets in which the sampling unit can be considered an isolated and well delimited community as a single coherent functional unit. For example, ecological communities living in islands or fragments of habitats isolated from the rest by any type of matrix habitat that impedes connectivity or dispersal. Local/isolated communities within these datasets are of varying sizes, allowing for the study of the scaling of community structure with spatial extent. Datasets in this category include: fish-based food webs from temperate lakes in Canada; plant-ant mutualistic networks from islands in a river basin of the Amazonian rainforest of Brazil; plant-frugivore interaction networks involving tropical birds and plants in isolated fragments of the Brazilian Amazonian forest; plant-pollinator and host-parasitoid insect networks in fragmented (due to agricultural activities) calcareous grasslands in central Germany; and plant-leafminer-parasitoid interaction networks from forest fragments embedded in an agricultural matrix landscape in central Argentina.

Biogeographical. Datasets from this category consist in sampling units of similar sizes that span large (i.e., biogeographical) spatial scales. Depending on the specifics of each dataset, local communities can be comprised of either collection of species found in each location for which interactions have been inferred from literature review or expert knowledge; or, on the other hand, direct observations of ecological interactions at each locality. This type of datasets comprises: the European terrestrial vertebrate food web split among 10 biogeographical regions according to climatic characteristics and in which local communities are defined at the 10x10km grid level; the terrestrial vertebrate food web, also defined at the 10x10km grid level for the catalan Pyrenees; and plant-herbivore-parasitoid interaction networks observed on plants of the genus *Salix* spanning a large latitudinal gradient from Italy to northern Norway.

3.3.2 Building network-area relationships

To analyse how network structure changes across spatial scales we built NARs for each dataset described above. Depending on the data type the procedure used to generate the spatial scaling of network structure was different.

Replicates. For this category, the smallest spatial scale was considered to be a single sampling unit. Communities at larger spatial scales were defined by aggregating sequentially each of the sampling units available until the whole set of replicated samples had been considered. We analysed network structure at each step of the aggregation procedure. This aggregation procedure might be subject to bias due to the order in which sampling units (i.e., local communities) are aggregated to create larger spatial extents. To avoid this bias, we replicated the aggregation procedure 100 times for each of the datasets in this category. For each replicate the aggregation order was randomly generated.

Islands-Fragments. Sampling units within datasets in this category were considered to be independent ecological communities, and as such they were analysed independently. To build NARs using this data category thus, network properties were calculated for each of the islands (or fragments) available within each dataset and these were related to the size of the islands-fragments in their respective dataset. This allowed us to build NARs in which the spatial scaling is given by the natural variation in area sizes across the islands-fragments within each dataset.

Biogeographical. To build NARs for datasets within this category, an aggregation procedure similar to that described for the replicates was used. The smallest spatial scale was also considered to be a single sampling unit and larger spatial scales were generated by the aggregation of these sampling units. The fundamental difference between these data and the replicates is that biogeographical data span large spatial extents and, thus, they are subject to larger environmental gradients than those experienced by replicates. Therefore, given that all datasets were georeferenced, the aggregation was conducted following the latitudinal gradient from north to south to be able to discriminate the effect of the latitudinal gradient. Since we are interested in the spatial scaling across the biogeographical latitudinal gradient, we did not perform replicated aggregations of the local communities as we did for the replicates, but instead we perform the aggregation procedure only once. NARs thus emerge from the aggregation of local communities in southward latitudinal gradients. Two types of data comprise this category: those collected in the field from single locations across the latitudinal gradient; and those where species interactions were inferred from species occurrences and literature-based knowledge on the interactions. For the first type of data, we start the aggregation procedure from the northern sampling unit and we increase the spatial

scale by progressively aggregating all the sampling units following the latitudinal gradient. For the other type of data, a single sampling unit is defined as the 10x10 km cells on a gridded map. Larger spatial scales in this case are, thus, simulated by merging adjacent cells of the map in an increasing manner from north to south. For both types of data, we analysed network structure at each spatial scale to build NARs.

3.3.3 Network properties

To characterise the structure of the ecological communities at each spatial scale we analysed a suite of network properties that allowed us to explore the complexity of the network, its vertical diversity and its modularity. In addition, we analysed the spatial scaling of biotic specialization from both, the community and the species perspective.

At each spatial scale, we measured network complexity by analysing the number of species (S), the total number of links (i.e., biotic interactions; L) present in the community and the number of links per species (L/S). Additionally, we analysed for each dataset the relationship between species richness and the total number of links (i.e., links-species scaling relationship). We assessed network vertical diversity by analysing species richness across trophic levels and consumer:resource ratios (S_c/S_r). For this, we calculated the fraction of basal (B), intermediate (I) and top (T) species in food webs. Equivalently, for the case of bipartite networks, we quantified the fraction of resources and consumer species respectively. Notice that to compute consumer:resource ratios in food webs we considered as consumers all species that have at least one prey, and as resources all species having at least one predator. Thus, one species can be considered as both consumer and resource.

Biotic specialization was measured at the network level by computing the mean indegree (mean number of resources a consumer utilises; L/S_c) of the community (also known as generality). To quantify biotic specialization from the species perspective across spatial scales, we analysed not only the realised number of links they have in a given spatial scale but also the total number of links they have at the regional scale. That is, the total number of interactions a species has across all the sampling units of its corresponding dataset. As in chapter 2, we call this potential indegree (or potential diet breadth) and we calculated it by considering the aggregation of all sampling units within each dataset (i.e., regional scale or 'metaweb') and analysing the number of interactions each species has in the aggregation. Therefore, each species from a given dataset has a fixed potential indegree and analysing the spatial scaling of the mean potential indegree allows us to have a better perspective on the traits of the species (i.e., more or less biotic specialists) across spatial scales.

Finally, network modularity (M), allowed us to quantify the extent to which groups of species form highly connected groups within which more interactions are observed than to the rest of the network. Modularity was quantified using the modularity function (Q) proposed by Newman and Girman [225]:

$$Q = \frac{1}{2m} \sum_{i,j} (A_{ij} - P_{ij}) \delta(g_i, g_j)$$

where m is the number of edges in the network, A_{ij} are the adjacency matrix elements (1 if a link between vertices i and j exists and 0 otherwise), P_{ij} is the expected number of links between i and j (i.e., $k_i k_j / 2m$, with k the degree of a vertex), g_i is the compartment to which vertex i belongs (as described in [226]. $\delta(r, s) = 1$ if $r = s$ and 0 otherwise. Since this measure is most appropriate for unipartite networks, when looking at bipartite networks, we used a modified version of Q in which P_{ij} are the probabilities from a null model, which take into account the bipartite nature of the network, that an edge exists between vertices i and j , as proposed by Barber [226]. To calculate modularity in food webs (unipartite networks) we used the random-walk based algorithm walktrap [227] implemented in the R package *igraph* [228]. To calculate modularity in bipartite networks we employed the LPAwb+ community detection algorithm [229], implemented in the *bipartite* [230] package in R.

3.3.4 Statistical Analyses

After constructing NARs for each dataset, we analysed the resulting scaling patterns statistically by fitting to each network-area relationship power functions of the form: $N = cA^z$, where N corresponds to any of the network properties analysed, A is area size and c and z are the fitting parameters. The scaling exponents (z) obtained were then compared across different data and interaction types to determine whether generalities exist in NARs scaling. Power functions were fitted to data using the *nls* function in R. To assess the accuracy of the models we used the R^2 and p-values of the fitted statistical models.

Once a collection of all the scaling exponents across data types and network properties were obtained, we used box plots to look at the patterns in the distributions of scaling exponents. Differences among the distributions of scaling exponents across data and interaction types were quantified using Wilcox tests. Wilcox tests were conducted using the *wilcox.test* function in R. To explore relationships between the spatial scaling of different network properties we plotted scaling exponents against each other and performed linear regression to assess the significance of the relationships.

3.4 RESULTS

3.4.1 Are there universal Network-Area Relationships?

The spatial scaling of network complexity metrics (i.e. number of species, links and links per species) showed universal patterns across data types and interaction types (Figure 23; Appendix S3.2). The number of species, links and links per species increased with area size following a power law regardless of the system characteristics (i.e., data category and interaction type). However, the z-exponents of the power law varied significantly across data types for the three complexity metrics analysed. Species richness increased with area significantly slower in islands (mean z-exponent = 0.14 ± 0.06) than in the replicates category (mean z-exponent = 0.32 ± 0.13), which did not show a significant difference with the biogeographical data (mean z-exponent = 0.28 ± 0.19) (Figure 23; Table 3; Appendix S3.3). Similarly, the number of links and the number of links per species increased with area slower in the islands than in the rest of the data categories, which showed no significant differences between them (Figure 23; Table 3; Appendix S3.3). We observed no significant differences in the spatial scaling of any of the complexity metrics between interaction types (Appendix S3.3).

Table 3. Pairwise comparison results of the z-exponents between data types. Comparisons using Wilcoxon rank sum tests of the z-exponents of the power relationships (in order): species-area, links-area, links/species-area, links-species, indegree-area, potential indegree-area. ‘Bio.’ corresponds to the biogeographical data category; ‘Rep.’ to the replicates data category; Island correspond to islands-fragments data category.

	z SAR		z LAR		z L.SAR		z L-S		z Indegree		z Potential	
	Island	Rep.	Island	Rep.	Island	Rep.	Island	Rep.	Island	Rep.	Island	Rep.
Bio.	0.103	0.079	0.063	0.371	0.001	0.347	0.001	0.008	0.296	0.296	0.81	0.64
Rep.	0.008	/	0.047	/	0.001	/	0.005	/	0.099	/	0.65	/

The difference between the exponents of the power relationships between the number of species and the number of links with area indicates that in islands the increase in the number of links in relation to the increase in species richness is slower than in the other data types. For all datasets, the scaling of the number of links with species richness followed a power law, with z-exponents ranging from 1.2 and 1.9 (Figure 24a; Appendix S3.4). Yet, the z-exponents for the links-species relationship varied significantly across data types and interaction types (Appendix S3.4). Biogeographical data showed the faster increase

of the number of links with species richness (mean z-exponent = 1.79 ± 0.20), followed by replicates (mean z-exponent = 1.60 ± 0.20) and islands (mean z-exponent = 1.31 ± 0.06), that showed the slowest increase. Interestingly, food webs showed a faster increase in the number of links with species richness than the other types of interaction (i.e. mutualistic and antagonistic) (Figure 24a; Appendix S3.4). We observed a linear relationship between the scaling of both network properties with area (i.e., SAR and LAR z-exponents), indicating that the way species richness scales with area highly determines the spatial scaling of the number of links (Figure 24b; Appendix S3.4).

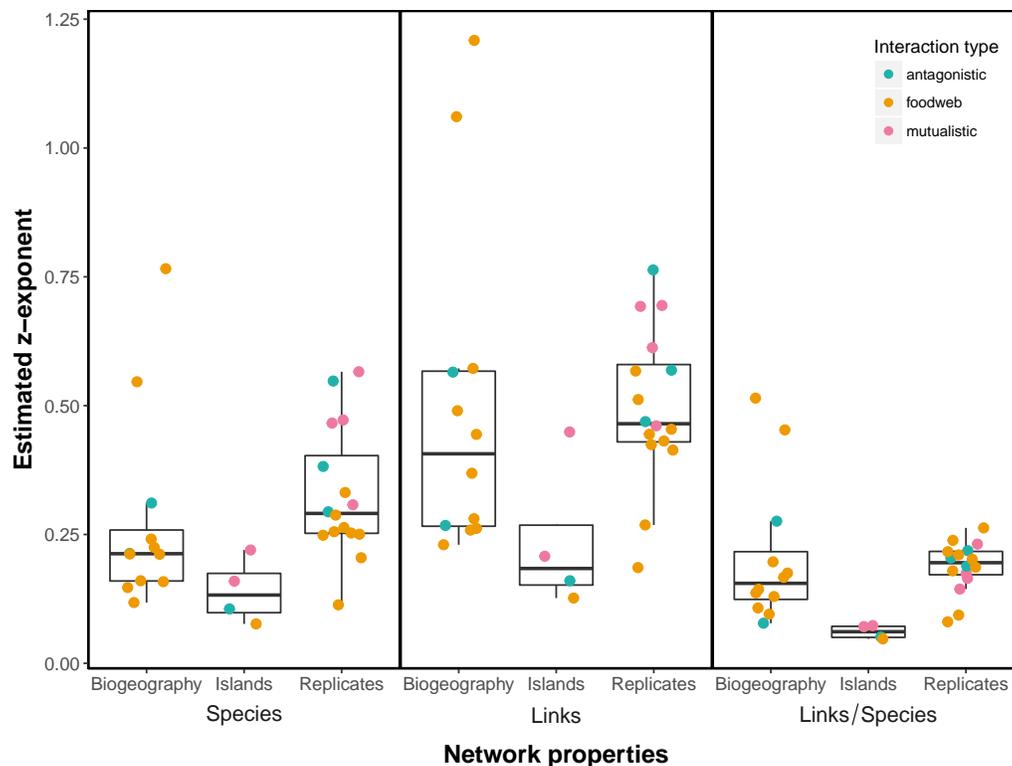


Figure 23. Spatial scaling of coarse-grained properties. Comparison of the z-exponents of the power law fit for the relationship between the number of species, the number of links and number of links per species with area classified by data type. Colours represent the type of interaction. Blue: antagonistic interactions; orange: food webs; pink: mutualistic interactions.

The spatial scaling of species richness per trophic level did not show universal patterns (Appendix S3.2). Although we observed variation in the species-area relationship across trophic levels, we did not observe a consistent increase nor decrease of the power exponent with trophic level for any data type or interaction type. Similarly, consumer:resource ratio did not change universally with area. We observed changes in both directions (i.e., increase or decrease of the consumer:resource ratio) with area, regardless of the type of data or interaction (Appendix S3.2).

Network modularity did not show strong variations across spatial scales for all the datasets analysed (Appendix S3.2). Yet, the spatial scaling of modularity was negative for all datasets that showed a significant variation with area, which included datasets from all data types and all interaction types (Appendix S3.2).

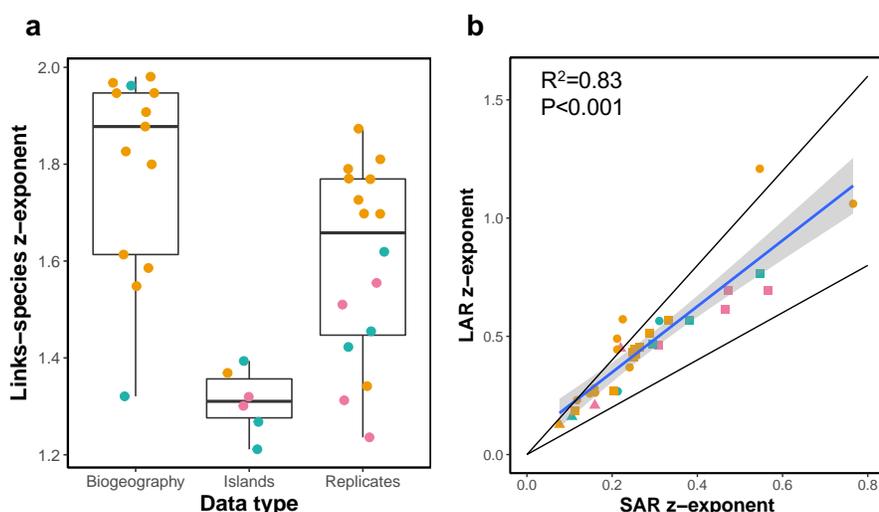


Figure 24. Links-species relationship. (a) Comparison of the z-exponents of the power law fit for the relationship between the number of links and species richness classified by data type. Colours represent the type of interaction. Blue: antagonistic interactions; orange: food webs; pink: mutualistic interactions. (b) Relationship between the z-exponents of the power law fit for the relationship between the number of links with area (LAR z-exponent) and the z-exponents of the power law fit for the relationship between the number of species with area (SAR z-exponent). Each point corresponds to a different dataset. Colours represent the type of interaction as described above. Shapes represent the data category. Dots: biogeography data; triangles: islands; squares: replicates. The blue line represents a linear model fit to data points and the two black lines represent the boundaries for the links-species relationship (i.e., z-exponent=1 for the lower line and z-exponent=2 for the upper line). Shaded areas show 95% confidence intervals.

3.4.2 Is biotic specialization changing across spatial scales?

Network mean indegree (i.e., mean number of links per consumer) increased with area size following a power law for all data types and interaction types, with some exceptions in the islands category, which did not show a significant change of network mean indegree with area (Figure 25a; Appendix S3.2). Therefore, consumer species had more resources as area size increased. Mean indegree increased with area slower in islands (mean z-exponent = 0.09 ± 0.06) than in the biogeographical data (mean z-exponent = 0.19 ± 0.13) and the replicates category (mean z-exponent = 0.22 ± 0.11). However, we did not observe significant differences between them (Figure 25a; Table 3). Similarly, we observed no significant differences in the spatial scaling of mean indegree between interaction types (Appendix S3.3).

The spatial scaling of mean indegree was associated to changes in the consumer:resource ratio with area (Figure 25b). Stronger changes in the mean indegree with area (i.e., high mean indegree z-exponent) were associated to a decrease in the consumer:resource ratio with area (i.e., negative values for ratio z-exponent). Therefore, we observed a negative relationship between the spatial scaling of mean indegree and the spatial scaling of consumer:resource ratio (Figure 25b). That is, larger increases in the number of resources than in the number of consumers with area promoted a larger increase in the number of links per consumer (Figure 25b).

Conversely, mean potential indegree (i.e., mean number of links each consumer has in the corresponding metaweb) decreased with area size for all data categories (Figure 25c; Appendix S3.2). Thus, consumer species with more resources at the regional scale (i.e., metaweb) were found in smaller areas regardless of the data type, suggesting that species that have less potential resources (i.e., more specialists) were increasingly sampled as area size increased (Figure 25c). The decrease of the mean potential indegree with area size was stronger in antagonistic and mutualistic bipartite networks than in foodwebs (Appendix S3.3).

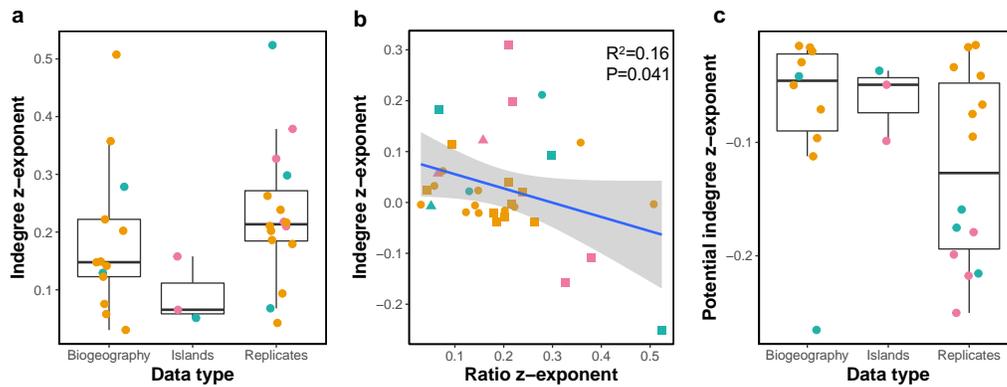


Figure 25. The spatial scaling of biotic specialization. (a) Comparison of the z-exponents of the power law fit for the relationship between mean indegree with area size classified by data type. Colours represent the type of interaction. Blue: antagonistic interactions; orange: food webs; pink: mutualistic interactions. (b) Relationship between the z-exponents of the power law fit for the relationship between mean indegree with area and the z-exponents of the power law fit for the relationship between the consumer:resource ratio with area. Each point corresponds to a different dataset. Colours represent the type of interaction as described above. Shapes represent the data category. Dots: biogeography data; triangles: islands; squares: replicates. The blue line represents a linear model fit to data points. (c) Comparison of the z-exponents of the power law fit for the relationship between mean potential indegree with area size classified by data type. Colours represent the type of interaction as described above. Notice that all z-exponents are negative indicating the decrease of the mean potential indegree with area size.

3.5 DISCUSSION

We have used a large collection of empirical datasets to show that not only species richness increases with area size but also the complexity of the network of biotic interactions in which species are embedded. The number of links and links per species increased with area size following a power law regardless of the data category (i.e., replicates, islands or biogeographical data) or interaction type (i.e., bipartite mutualistic and antagonistic or multi-trophic webs). Similarly, network mean indegree increased universally with area size, indicating that on average consumers are using more resources as area increases. However, mean potential indegree (i.e., mean number of resources a consumer has at the regional scale) decreased across spatial scales for all data categories and interaction types, suggesting that specialist species require larger areas to be present.

The use of multiple types of data allowed us to determine whether the observed network-area relationships (NARs) were universal and how their specific shape was affected by the underlying ecological processes captured by each data type (Figure 22). Data structured as replicates provide direct information on the effects of β -diversity of both species composition and its biotic interactions for the spatial scaling of community structure [94], [218], [231]. Biotic interactions can experience spatial turnover independently from species occurrences given that the prevalence of an interaction between two species is not only determined by their co-occurrence in space, but also by the surrounding environment [134], [135], [137] and their relative abundances. Thus, the larger the β -diversity of species composition and biotic interactions, the larger the changes observed in network structure across spatial scales. Similarly, data structured as replicates but across large environmental gradients (i.e., biogeographical data), provide insights on the presence of multiple species pools along the geographical gradient (i.e., when crossing biogeographical boundaries of migration) that might be the result of separate evolutionary histories [81], [218], and that can promote changes in the biotic interactions between species and in the structure of ecological networks. Finally, data on islands or fragments are more strongly dominated by colonisation-extinction dynamics that determine species composition for a given area size [80], and its trophic interactions [86]–[88], [93].

Although all our data categories followed a power law to describe the increase of network complexity with area size, they did show differences in most of the scaling exponents. Replicates generally showed the fastest increase of network complexity with area while islands showed the slowest, especially for the spatial scaling of the number of links per species (Figure 23). This indicates that in islands species gain less interactions as area size increases, suggesting that the turnover of links (i.e., Link β -diversity) independently of the turnover of species composition, might be an important determinant of the slope of the spatial scaling of the number of links per species. Regardless of area, the scaling of the number of links with species richness has been widely studied in food web ecology [8], [104], [106]–[108]. The scaling exponent of the number of links with species is, by definition, constrained between 1 and 2. That is, the minimum number of links in a network is equal to species richness - 1 (z-exponent = 1); and the maximum number of links corresponds to a fully connected network (z-exponent = 2) (see [104], [107]). As previously shown in other empirical studies [8], [108], we found the scaling of the number of links with species richness to fall between these two extremes. Yet, islands showed the slowest increase of the number of links when increasing species number (Figure 24a), suggesting that ecological communities in islands are less complex when they become larger. Following the constraints mentioned above, we expected a universal relationship between the spatial scaling of species richness and the spatial

scaling of the number of links to emerge (Figure 24b), which suggest that the increase of the number of links with area size could be predicted by the spatial scaling of the number of species.

Another facet of network complexity is the mean number of resources used by each consumer (i.e., mean indegree), which informs us about the degree of specialization of the community. Biotic specialization is influenced by multiple ecological and evolutionary processes [118], [232]–[234], and it is at the bases of species population dynamics, distribution and diversity [235]–[238]. For instance, specialist species have been shown to be more vulnerable to extinction and to environmental perturbations [234], [239]–[241]. Thus, understanding the spatial scaling of biotic specialization is fundamental to improve our knowledge on the spatial distribution of species depending on their degree of specialization and, therefore, to better assess their vulnerability to perturbations such as habitat loss or fragmentation. We found that mean network indegree increased with area size universally for all our data categories (Figure 25a). Given the relationship between mean indegree (L/S_c) and the number of links per species (L/S), is expected that the difference between the two is determined by the consumer:resource ratios (S_c/S_R). We did not observe a clear pattern for the consumer:resource ratio with area size across datasets, which resulted in differing patterns of the spatial scaling of mean network indegree when normalised by the number of links per species. Similarly, we did not observe consistent differences in the species-area relationship across trophic levels. Although previous studies showed a consistent increase of the slope of SARs with trophic level, and its further consequences for the structure of the network [88], [95], [96], [98], our results suggest that the spatial scaling of the consumer:resource ratio might be system specific.

Aside from the information on biotic specialization from the network perspective, we can assess the degree of biotic specialization of each species at the regional spatial scale (i.e., potential indegree) and evaluate how species are distributed across spatial scales based on this trait. As previously shown theoretically in chapter 2 [242], we observed that potential indegree decreased universally with area size (Figure 25c). This gives us different insights depending on the data category analysed. For islands, the decline of the mean potential indegree with area size reflects the stronger effect of the trophic constraint on specialist species at small area size [86], [93], [242]. That is, consumer species having a larger set of resources at the regional scale have a higher probability of finding one of the required resources at smaller spatial scales, where the total number of species is smaller. As area size increases the total number of species increases, and therefore, the probability for specialist species of finding a required resource to colonize and persist, also increases [86], [93], [242]. For replicates and biogeographical data, the decrease of the potential indegree across spatial scales indicates that generalist species have a higher prevalence

across space. Given the procedure we used to generate NARs for these data categories, the decline in potential indegree indicates that the number of specialist species increased as the number of sampling units aggregated increased. For this to happen, generalist species need to be systematically found at the first steps of the aggregation procedure (i.e., small area size), indicating their higher prevalence across all the sampling units. Therefore, specialist species have narrower spatial distributions and, in consequence, might be more vulnerable to environmental perturbations [239]–[241], [234].

Although we have shown some universalities in the spatial scaling of network structure, further research is needed to fully understand how ecological communities change across spatial scales. Particularly challenging is to assess the changes in species interactions strength within a community across spatial scales. The spatial scaling of quantified networks could provide new perspectives on ecosystem functioning and stability at different spatial scales. Similarly, incorporating habitat heterogeneity explicitly into the analyses of the spatial scaling of network modularity, would elucidate the effect of area size on this facet of network structure given that heterogeneous landscapes are likely to promote the emergence of compartments in the network [200], [201]. Finally, more studies should aim to disentangle all the possible mechanisms affecting the slopes of NARs as its been widely done for SARs [94].

Author contributions:

NG and JMM designed research. NG and ML analysed the data. NG, ML and JMM conducted research with feedback from all the co-authors. NG wrote the manuscript and JMM contributed to the edition. All authors contributed with data and discussions.

SUPPLEMENTARY MATERIAL CHAPTER 3

Content

- **Appendix S3.1.** Datasets description.
- **Appendix S3.2.** Power function fits for NARs.
- **Appendix S3.3.** Pairwise comparison results for interaction types.
- **Appendix S3.4.** Power function fits for the Links-species relationship.

Appendix S3.1. Datasets specification. Description of different aspects of the datasets used to build networks across spatial scales (i.e., Network-Area Relationships), including locations, area sizes, and sampling methodologies. To follow the same order of the manuscript they are presented grouped into the data type categories used in the main text: replicates, islands-fragments, and biogeographical. In brackets is shown the name that has been assigned to each dataset and that will be used in the following appendixes.

Replicates.

1-3. Plant-pollinator and host-parasite interaction networks in mildly degraded natural Mediterranean forest in the Garraf Natural Park, Catalunya, Spain. (Garraf_pp, Garraf_pp2, Garraf_hp)

Three independent datasets were collected within this same area. These are identified by numbers in each section. 1 & 2 = Plant-pollinator networks, 3 = Host-parasite networks.

- **Study area:** Garraf Natural Park, Catalunya, Spain
- **Interaction types:** Plant-pollinator and host-parasite (Cavity-nesting bee/wasps and their cleptoparasites, parasitoids and nest predators) interactions.
- **Type of system:** Semi-natural habitat of Mediterranean forest.
- **Number and extent of replicated patches:**
 - 1.- 40 local patches of the same size (40 x 30 m) within a homogeneous landscape connected through dispersal. Total area: 40 Km². Distance between patches: 520 to 1440 m.
 - 2.- 21 local patches of the same size (40 x 40 m) within a homogeneous landscape connected through dispersal. Total area: 32 Km². Distance between patches: 585 to 1345 m.
 - 3.- 25 local patches. Total area: 33 Km². Distance between patches: 585 to 1354 m.
- **Number of networks:** 1 plant-pollinator or 1 host-parasitoid network per patch. This yields a total of 86 networks
- **Type of networks:** Bipartite.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:**
 - 1.- 170 pollinator and 24 plant species. 3577 individual contacts spread across a total of 325 inter-specific interactions.
 - 2.- 303 pollinator and 23 plant species. However, information on interactions available only for 200 species. 900 interactions.

3.- 41 host and 26 parasite species. 654 individuals parasitized spread across a total 72 inter-specific interactions.

- **Sampling procedure (of species and interactions):**

Plant-pollinator interactions:

1.- Counted number of visits per open flower by each pollinator species.

2.- Interactions inferred from interactions observed during four years in other plots within the same landscape.

Host-parasite interactions:

3.- Nests of hosts were collected from trap-nests to obtain the parasite species using the nest. An interaction was considered when a parasite species was observed in a host's nest.

- **Publication reference:** Unpublished.

4. Host-parasite interaction networks within a mosaic of forest/agricultural landscape in Olot, Catalunya, Spain. (Olot)

- **Study area:** Olot, Catalunya, Spain
- **Interaction types:** Host-parasite (Cavity-nesting bee/wasps and their associated parasites) interactions
- **Type of system:** Mosaic landscape of mixed forest and extensive agricultural land
- **Number and extent of replicated patches:** 14 local patches. Total area: 100 Km². Distance between patches 1.4 to 13 Km.
- **Number of networks:** 1 host-parasite network per patch. This yields a total of 14 networks
- **Type of networks:** Bipartite
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 29 host and 20 parasitoid species. 1695 contacts (cells parasitized) spread across a total of 80 inter-specific interactions.
- **Sampling procedure (of species and interactions):** Nests of hosts were collected from trap-nests to obtain the parasite species using the nest. An interaction was considered when a parasite species was observed in a host's nest.
- **Publication reference:** Unpublished.

5. Plant-pollinator interaction networks within dense forest in Montseny Natural Park, Catalunya, Spain. (Montseny)

- **Study area:** Montseny Natural Park, Catalunya, Spain
- **Interaction types:** Plant-pollinator interactions
- **Type of system:** Local patches (clearings) within a dense forest matrix
- **Number and extent of replicated patches:** 18 local patches of the same size (25 x 25 m). Total area: 18.7 Km². Distance between patches 550 to 2050 m.
- **Number of networks:** 1 plant-pollinator network per patch. This yields a total of 18 networks
- **Type of networks:** Bipartite.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 194 pollinator and 61 plant species. 8605 individual flower visits distributed among a total 873 unique inter-specific interactions.
- **Sampling procedure (of species and interactions):** Counted number of visits per open flower by each pollinator species.
- **Publication reference:** Unpublished.

6. Plant-pollinator networks in Nahuel Huapi National Park, Argentina. (Nahuel)

- **Study area:** Nahuel Huapi National Park and surrounding areas in Río Negro, Argentina
- **Interaction types:** Plant-pollinator interactions (flower visits).
- **Type of system:** Eight sites with native temperate forest, four grazed with domestic cattle and four ungrazed, located in an area of ca. 20 km x 50 km.
- **Number and extent of replicated patches:** Eight sites of 6-12 ha.
- **Number of networks:** 8, one per site.
- **Type of networks:** Bipartite
- **Taxonomic resolution of the nodes:** Species level
- **Total number of species and links at the regional scale:** 14 plants, 90 pollinators, 164 links, 5285 flower visits.
- **Sampling procedure (of species and interactions):** Data were collected throughout one flowering season, with weekly sampling of each site (a pair of sites per day), with multiple 5 min observation periods per site and date. Interactions were determined by observed visits to flowers. Links are quantified as the total number of visits recorded in the study.

- **Publication reference:** Vázquez, D. P. & Simberloff, D. 2003. Changes in interaction biodiversity induced by an introduced ungulate *Ecology Letters*, 6, 1077-1083

7. Trophic marine intertidal networks in the Sanak Archipelago, Alaska. (Sanak)

- **Study area:** The Sanak Archipelago lies in the Eastern Aleutian Islands, south of the Alaska Peninsula, in the North Pacific Ocean.
- **Interaction types:** Trophic interactions.
- **Type of system:** The coastline contains a mix of semi-exposed rocky intertidal habitats interspersed with protected sedimented and boulderstrewn shores.
- **Number and extent of replicated patches:** The data used consists of 339 quadrants of 0.25m² along 39 transects that were laid across the intertidal zones around the Sanak Islands. Transects spanned the entire intertidal zone, and were placed perpendicular to the shoreline at 300m intervals.
- **Number of networks:** 1 food web per quadrant (i.e., 339 local food webs).
- **Type of networks:** Food webs.
- **Taxonomic resolution of the nodes:** Nodes span the entire range from species to phyla. Taxa were identified to the lowest possible resolution in the field. Some taxa were lumped into groups.
- **Total number of species and links at the regional scale:** 100 species and 502 links.
- **Sampling procedure (of species and interactions):** direct observation of the species presences. To determine interactions between species, mixture of direct observation, gut content analysis, stable isotope analysis, literature searches and discussion with experts.
- **Publication reference:** Wood, S. A., Russell, R., Hanson, D., Williams, R. J., & Dunne, J. A. (2015). Effects of spatial scale of sampling on food web structure. *Ecology and evolution*, 5(17), 3769-3782.

8. Trophic marine intertidal networks in the Bristol Channel, UK. (Bristol)

- **Study area:** Four study sites composed by archipelagos of salt marsh islands located in the intertidal mudflats along the Bristol Channel in the southwest of England.
- **Interaction types:** Plant-pollinator, plant-herbivore, predator-prey interactions.
- **Type of system:** salt marsh islands located in four archipelagos on intertidal mudflats.
- **Number and extent of replicated patches:** 39 small salt marsh islands of 0.2–2 m² in size. Larger islands were excluded to be able to treat the data as replicates of the same size.
- **Number of networks:** 1 food web per island (i.e., 39 food webs)

- **Type of networks:** Food webs.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 57 species and 175 links.
- **Sampling procedure (of species and interactions):** direct observation of the species presences. To determine interactions between species, mixture of direct observation, gut content analysis, stable isotope analysis, literature searches and discussion with experts.
- **Publication reference:** Montoya, D., Yallop, M. L., & Memmott, J. (2015). Functional group diversity increases with modularity in complex food webs. *Nature communications*, 6, 7379.

9. Host-specific gallers and leaf-miners in pedunculate oaks in Finland. (*Quercus*)

- **Study area:** natural communities of specialist insect-herbivores and their natural enemies on the pedunculate oak, *Quercus robur* in the southwest coast of Finland.
- **Interaction types:** Host-parasitoid interactions (host-specific gallers and leaf-miners in pedunculate oaks)
- **Type of system:** Naturally fragmented landscape of oak trees in the archipelago of SW Finland.
- **Number and extent of replicated patches:** 22 oak trees.
- **Number of networks:** 1 per tree (i.e., 22 networks).
- **Type of networks:** Bipartite.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 85 species and 135 links.
- **Sampling procedure (of species and interactions):** sampling was conducted three times in 2006: in May-June, in late July, and in September in 2006. During each sampling event, a standardized volume of foliage (30 half-meter branches per tree) was collected with the aid of a pole pruner, and all galls and leaf-mines present were recorded. Interactions were quantified by rearing of predators.
- **Publication reference:** Kaartinen, R., & Roslin, T. (2011). Shrinking by numbers: landscape context affects the species composition but not the quantitative structure of local food webs. *Journal of Animal Ecology*, 80(3), 622-631.

10. Soil food webs Christian mulder (Soil 1-7)

- **Study area:** Netherlands.
- **Interaction types:** Trophic interactions.
- **Type of system:**

- 19 Scots pine forests, used for traditional agroforestry.
 - 10 certified organic grasslands (including mixed and bio-dynamic regimes), using compost/farmyard manure and no biocides, averaging 60 ha.
 - 19 conventional farms, using mineral fertilisers, with a much smaller amount of farmyard manure, averaging 45 ha.
 - 20 semi-intensive farms, using both organic and mineral fertilisers, averaging 25 ha.
 - 19 intensive farms, using biocides and fertilisers, averaging 20 ha.
 - 28 multicropping fields.
 - 9 abandoned meadows.
- **Number and extent of replicated patches:** see above.
 - **Number of networks:** 1 network per site: 125 networks.
 - **Type of networks:** Food webs.
 - **Taxonomic resolution of the nodes:** genus level.
 - **Total number of species and links at the regional scale:**
 - 130 species; 2647 links
 - 181 species; 5174 links
 - 136 species; 3609 links
 - 144 species; 3888 links
 - 103 species; 2177 links
 - 101 species; 2002 links
 - 102 species; 2044 links
 - **Sampling procedure (of species and interactions):**

Microarthropods were collected in a randomized block design and their four-fold cores (diameter 5.8 cm×5 cm) were kept separate until behavioural extraction using the Tullgren high-gradient canister method with a low wattage bulb.

Enchytraeids were sampled using six-fold cores (diameter 5.8 cm×15 cm, 6 rings of 2.5 cm height each), extracted using wet funnel extraction, identified, measured and counted. Lumbricids were recovered manually, identified, weighted and counted.

Nematodes were extracted from 100 g soil using elutriation, sieving and cottonwool extraction. All individuals within two clean 10 ml water suspensions were screened, counted with a stereomicroscope and fixed in 4% formaldehyde. Per sample, at least 150 individuals were identified at genus level by light microscopy (400–600×) and assigned to feeding habits.

Soil community structure was described using food-web data with M (dry body mass in μg), N ($\text{animals}/\text{m}^2$) and B (dry biomass in $\mu\text{g}/\text{m}^2$, i.e. $\log(B)=\log(N)+\log(M)$). A guild-lumped web was established for each site by taking the sub-predation-matrix determined by the trophic guilds that

were present. The presence or absence, but not the quantitative extent, of consumer–resource links was established using additional information from the literature.

- **Publication reference:** Mulder C, Den Hollander HA, Hendriks AJ (2008) Aboveground Herbivory Shapes the Biomass Distribution and Flux of Soil Invertebrates. PLoS ONE 3(10): e3573. <https://doi.org/10.1371/journal.pone.0003573>

Fragments.

1-2. Plant-pollinator and host-parasitoid interaction networks on fragmented calcareous grasslands of Germany. (Gottin_pp, Gottin_hp)

Three independent datasets were collected within this same area.

- **Study area:** Göttingen, central Germany
- **Interaction types:** Plant-pollinator and host-parasitoid interactions
- **Type of system:** Calcareous grassland. Semi-natural habitat of high conservation value due to their high biodiversity (plants and insects in particular). These grasslands are heavily fragmented due to agricultural landscape simplification and intensification.
- **Number and extent of fragments:** 32 fragments. Area size of fragments ranged from 314 m² to 51,395 m².
- **Number of networks:** 1 plant-pollinator and 1 host-parasitoid network per fragment. This yields a total of 64 networks
- **Type of networks:** Bipartite
- **Taxonomic resolution of the nodes:** Species level in most cases (some hosts or parasitoids identified to genus level and then assigned to morphospecies).
- **Total number of species and links at the regional scale:** 5552 plant-pollinator interactions among 101 plant species and 138 pollinator species. 1812 host-parasitoid interactions among 17 host species and 21 parasitoid species.
- **Sampling procedure (of species and interactions):**

Plant-pollinator networks: Flower visitors (wild bees and hoverflies; assumed to be pollinators of visited plants) were sampled via five-minute-transect walks six times from April to September 2004 within a 4 m corridor. To achieve adequate sample sizes for the differently sized grassland fragments, we conducted four of the 5-min-transects (total = 20 min) in eleven small fragments (314–1,133 m²), eight 5-min-transects (total = 40 min) in 13 medium fragments (1326–7887 m²),

and twelve 5-min-transects (total = 60 min) in eight large fragments (11,528–51,395 m²). Data from the 5-min-transects of all six sampling events were pooled per grassland fragment. Specimens were either identified on the wing or caught with a net and identified in the lab. The plant species visited was recorded for each specimen.

Host-parasitoid networks: Parasitoids/parasites and hosts were sampled using trap nests at the same sites. Trap nests consisted of bundles of reed internodes of common reed *Phragmites australis* (about 150–180 reed internodes of 2–10 mm diameter in plastic tubes of 10 cm diameter per trap nest) exposed at a height of 100–120 cm. Depending on the fragment size, 4–6 wooden posts with 2 trap nests each were used: 4 posts (8 trap nests) in 11 small fragments, 5 posts (10 trap nests) in 13 medium fragments, 6 posts (12 trap nests) in eight large fragments. The trap nests were spread regularly over study sites and exposed at the beginning of the flowering period (mid-April) until autumn (beginning October). Afterwards, trap nests were stored in a climate chamber at 4°C and occupied reed internodes were opened. For each nest, the number of brood cells and number of parasitized cells were recorded. We identified host and parasitoid identities to genus or species level as far as possible using larvae and nest characteristics. Because *Osmia rufa* overwinter as adults, these cocoons were opened to check for parasitoids. All other nests were stored separately in test tubes closed with a wad of cotton wool. Tubes were exposed to room temperature (ca. 20°C) to end diapause. Reared adults were identified to species level.

- **Publication reference:** Grass, I., Jauker, B., Steffan-Dewenter, I., Tscharrntke, T., & Jauker, F. (2018). Past and potential future effects of habitat fragmentation on structure and stability of plant–pollinator and host–parasitoid networks. *Nature ecology & evolution*, 1.

3. Plant-leafminer-parasitoid networks from central Argentina. (Chaco)

- **Study area:** Chaco Serrano District in Argentina, belonging to the most extensive dry forest in South America. The characteristic vegetation is low, open woodland, with a tree layer, shrubs, herbs and grasses, and many vines and epiphytic bromeliads.
- **Interaction types:** Plant-herbivore-parasitoid interactions
- **Type of system:** Woodland sites in a fragmented semi-natural landscape. The woodlands are mainly used for cattle grazing, and are embedded in an agricultural matrix largely dominated by wheat in winter and soy or maize in summer.
- **Number and extent of sites:** 15 woodland sites ranging in area size from 0.13ha to 29.53ha.
- **Number of networks:** 15 networks, one per site.
- **Type of networks:** Unipartite.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 470 species and 1235 links.

- **Sampling procedure (of species and interactions):** At each site, all mined leaves detected were collected along five 50 long, 2 m wide and 2 m high transects (100 m²) in two occasions (November-December 2002 and February-March 2003) within peak period of leafminer activity. Mined leaves were taken to the laboratory and reared adult leafminers and parasitoids, which were identified and counted.
- **Publication reference:** Cagnolo, L., Salvo, A., & Valladares, G. (2011). Network topology: Patterns and mechanisms in plant-herbivore and host-parasitoid food webs. *Journal of Animal Ecology*, 80(2), 342-351. Retrieved from <http://www.jstor.org/stable/41059064>

4. Ant-plant mutualistic interactions in central Amazonia. (Balbina)

- **Study area:** Sub-montane dense rainforest surrounding the Balbina Dam in Central Amazon.
- **Interaction types:** Amazonian ant-myrmecophyte plants.
- **Type of system:** Continuous tropical forest plots and fragments surrounded by water matrix.
- **Number and extent of sites:** 19 island-fragments from 2.55 to 1466 ha.
- **Number of networks:** 19, one per site.
- **Type of networks:** Bipartite.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 13 plant spp, 27 bird spp, 424 interactions at the metaweb. (Mean number of species in local communities: 7.26; Mean number of links in local communities: 13.58).
- **Sampling procedure (of species and interactions):** Interactions sampled along transects (600x5m), determined by the presence of ant colonies within domatia, and quantified if the same interaction was repeated within sites.
- **Publication reference:** Emer, C., Venticinque, E. M., & Fonseca, C. R. (2013). Effects of dam-induced landscape fragmentation on Amazonian ant-plant mutualistic networks. *Conservation Biology*, 27(4), 763-773.

5. Bird-plant interactions in the Brazilian Atlantic forest. (Bird.displ)

- **Study area:** South-East Brazilian Atlantic Forest.
- **Interaction types:** Bird seed-dispersal interactions.
- **Type of system:** Fragments of tropical forest surrounded by terrestrial matrix that includes crop plantations, pastures and urban areas.
- **Number and extent of sites:** 8 fragments ranging in area sizes from 0.6 ha to 30 ha.
- **Number of networks:** 8, one per fragment.

- **Type of networks:** Bipartite.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 324 plant spp, 169 bird spp, 2528 interactions at the metaweb (Mean number of species in local communities: 62.56; Mean number of links in local communities: 465.38).
- **Sampling procedure (of species and interactions):** Interactions determined and quantified based on local observations and diet sampling (faeces). This dataset compiles independent studies, from different authors in different years, and slightly variable methodologies.
- **Publication reference:** Emer, C., Galetti, M., Pizo, M. A., Guimarães Jr, P. R., Moraes, S., Piratelli, A., & Jordano, P. (2018). Seed-dispersal interactions in fragmented landscapes—a metanetwork approach. *Ecology letters*, 21(4), 484-493.

6. Trophic networks of the system of lakes in Canada. (lakes)

- **Study area:** Sampled lakes occur across an area of 450,000 km² in Ontario, Canada.
- **Interaction types:** Trophic interactions.
- **Type of system:** System of lakes.
- **Number and extent of sites:** 128 lakes ranging in area sizes from 40 ha to 83047.9 ha.
- **Number of networks:** 128, one per lake.
- **Type of networks:** Unipartite.
- **Taxonomic resolution of the nodes:** Species level.
- **Total number of species and links at the regional scale:** 68 species and 1775 links.
- **Sampling procedure (of species and interactions):** The lake data derived from the Province of Ontario's Broad-scale Monitoring (BsM) fish database, with all lakes surveyed for species richness (number of fish species per lake), species identity, numbers of fish per species per lake based on standardized netting protocols among all lakes, and a range of abiotic and lake morphological data. Species interactions were determined via gut content analyses.
- **Publication reference:** MacDougall, A. S., Harvey, E., McCune, J. L., Nilsson, K. A., Bennett, J., Firn, J., ... & McMeans, B. (2018). Context-dependent interactions and the regulation of species richness in freshwater fish. *Nature communications*, 9(1), 973.

Biogeographical.**1. Plant-herbivore and host-parasitoid interactions observed on willow tree species (*Salix spp.*) across Europe (Kopelke et al. *Ecology* 2017) (*Salix1*, *Salix2*)**

- **Study area:** Europe - from Italy in the south to Northern Norway
- **Interaction types:** Plant-herbivore and host-parasitoid interactions
- **Type of system:** Different habitats where species belonging to the *Salix* genus are found
- **Number and extent of sites:** 641 sites. Area size of sites varied between 0.01 and 1 ha depending on the size of individual trees
- **Number of networks:** 1 plant-herbivore and 1 host-parasitoid network per tree. This yields a total of 641 networks of each type.
- **Type of networks:** Bipartite
- **Taxonomic resolution of the nodes:** Trees and herbivores are resolved to the species level. All trees belong to the *Salix* genus. All herbivores are galling sawflies. Parasitoids are sometimes resolved to the genus level.
- **Total number of species and links at the regional scale:** 52 species of trees from the *Salix* genus, 96 species of sawflies (herbivores), and 126 parasitoid taxa.
- **Sampling procedure (of species and interactions):** Collection and counting of galls produced by the galling sawflies on the trees to identify the herbivore species, and rearing of parasitoids in the laboratory to identify them.
- **Publication reference:** Kopelke, J. P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S., & Roslin, T. (2017). Food-web structure of willow-galling sawflies and their natural enemies across Europe. *Ecology*, 98(6), 1730-1730.

2. Trophic interactions between terrestrial vertebrates across Europe (unpublished). (Alpine, Anatolian, Arctic, Atlantic, Black Sea, Boreal, Continental, Mediterranean, Pannonian, Steppic)

- **Study area:** Europe - from Portugal in the west to the Ural Mountains in the east and from Iceland in the north to the Mediterranean Sea in the south. Divided into 10 biogeographical regions: Alpine, Anatolian, Arctic, Atlantic, Black Sea, Boreal, Continental, Mediterranean, Pannonian, Steppic.
- **Interaction types:** Trophic interactions.
- **Type of system:** All terrestrial habitats and biogeographical regions in Europe
- **Number and extent of sites:** Maps of the European bioregions were divided in 10 x 10 Km cells. The number of cells varied among bioregions and were always of the same size.

- **Number of networks:** 1 trophic network per aggregation of cells from 1 to the maximum number of cells per bioregion
- **Type of networks:** Unipartite
- **Taxonomic resolution of the nodes:** All terrestrial vertebrates were resolved to the species level
- **Total number of species and links at the regional scale:** 1140 species and 69724 links at the European level, without dividing by biogeographical regions.
- **Sampling procedure (of species and interactions):** Species distribution maps were obtained from expert knowledge and models of habitat cover (as explained in Maiorano et al. 2013) and interactions were collected from literature records (including atlas, books and research articles) and expert knowledge.
- **Publication reference:** Unpublished.

3. Trophic interactions between terrestrial vertebrates in the Pyrenees. (Pyrenees)

- **Study area:** southeastern slopes of the Pyrenees (Iberian Peninsula side), from the highest creeks in the centre of the mountain range to the Mediterranean Sea in the east, covering a región of 900000 ha with elevations between 255 and 3140 m.a.s.l.
- **Interaction types:** Trophic interactions.
- **Type of system:** All terrestrial habitats.
- **Number and extent of sites:** 92 cells of 10 x 10 Km.
- **Number of networks:** 1 trophic network per aggregation of cells from 1 to the maximum number of cells (i.e., 92 food webs).
- **Type of networks:** Unipartite
- **Taxonomic resolution of the nodes:** All terrestrial vertebrates were resolved to the species level.
- **Total number of species and links at the regional scale:** 212 species and 846 interactions.
- **Sampling procedure (of species and interactions):** **Species presence/absence was extracted** from public databases and extensive bibliography search. Interactions were inferred based on species co-occurrence in space and habitat.
- **Publication reference:** Lurgi, M., López, B. C., & Montoya, J. M. (2012). Novel communities from climate change. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 367(1605), 2913-2922.

Appendix S3.2. Power function fit for the relationship of each network property analysed with area size for each dataset. P-value significance is shown by: ° < 0.1, * < 0.05, ** < 0.01, *** < 0.001. We used nonlinear least squares (NLS) with the 'nls' function in R.

dataset	property	z-exponent	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	species	0.308	0.0018	173.98***	Replicates	mutualistic
Garraf_pp	species	0.566	0.0019	299.12***	Replicates	mutualistic
Montseny	species	0.472	0.0029	161.90***	Replicates	mutualistic
Nahuel	species	0.466	0.0032	143.51***	Replicates	mutualistic
Garraf_hp	species	0.548	0.0032	173.74***	Replicates	antagonistic
Olot	species	0.382	0.0034	111.26***	Replicates	antagonistic
Quecus	species	0.294	0.0019	153.14***	Replicates	antagonistic
Soil1	species	0.248	0.0015	168.26***	Replicates	foodweb
Soil2	species	0.288	0.0026	112.64***	Replicates	foodweb
Soil3	species	0.250	0.0014	180.22***	Replicates	foodweb
Soil4	species	0.255	0.0015	170.48***	Replicates	foodweb
Soil5	species	0.331	0.0052	63.94***	Replicates	foodweb
Soil6	species	0.253	0.0015	167.33***	Replicates	foodweb
Soil7	species	0.263	0.0017	157.62***	Replicates	foodweb
Bristol	species	0.113	0.0007	152.96***	Replicates	foodweb
Sanak	species	0.205	0.0005	399.25***	Replicates	foodweb
Gottin_pp	species	0.159	0.0181	8.80***	Islands	mutualistic
Gottin_hp	species	0.057	0.0386	1.49	Islands	antagonistic
Bird.disp	species	0.220	0.0628	3.50**	Islands	mutualistic
Balbina	species	0.142	0.0743	1.92°	Islands	mutualistic
Chaco	species	0.105	0.0209	5.05**	Islands	antagonistic
Lakes	species	0.076	0.0156	4.91**	Islands	foodweb
Pyrenees	species	0.241	0.0070	34.42***	Biogeography	foodweb
Alpine	species	0.546	0.0019	283.24***	Biogeography	foodweb
Mediterranean	species	0.158	0.0002	789.64***	Biogeography	foodweb
Steppic	species	0.225	0.0010	219.11***	Biogeography	foodweb
Boreal	species	0.160	0.0002	914.39***	Biogeography	foodweb
Continental	species	0.212	0.0007	319.18***	Biogeography	foodweb
BlackSea	species	0.147	0.0016	90.11***	Biogeography	foodweb
Atlantic	species	0.212	0.0007	310.46***	Biogeography	foodweb
Arctic	species	0.766	0.0030	257.98***	Biogeography	foodweb
Pannonian	species	0.033	0.0002	140.84***	Biogeography	foodweb
Anatolian	species	0.118	0.0004	299.74***	Biogeography	foodweb
Salix1	species	0.213	0.0037	58.18***	Biogeography	antagonistic
Salix2	species	0.311	0.0030	102.46***	Biogeography	antagonistic

dataset	property	z-exponent	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	links	0.461	0.0039	117.73***	Replicates	mutualistic
Garraf_pp	links	0.694	0.0024	286.16***	Replicates	mutualistic
Montseny	links	0.693	0.0043	162.02***	Replicates	mutualistic
Nahuel	links	0.612	0.0038	161.92***	Replicates	mutualistic
Garraf_hp	links	0.763	0.0047	163.87***	Replicates	antagonistic
Olot	links	0.569	0.0039	144.60***	Replicates	antagonistic
Quecus	links	0.469	0.0027	174.36***	Replicates	antagonistic
Soil1	links	0.431	0.0032	136.83***	Replicates	foodweb
Soil2	links	0.512	0.0050	102.23***	Replicates	foodweb
Soil3	links	0.414	0.0025	162.39***	Replicates	foodweb
Soil4	links	0.424	0.0030	140.13***	Replicates	foodweb
Soil5	links	0.567	0.0099	57.53***	Replicates	foodweb
Soil6	links	0.444	0.0032	140.27***	Replicates	foodweb
Soil7	links	0.454	0.0034	131.93***	Replicates	foodweb
Bristol	links	0.186	0.0019	96.19***	Replicates	foodweb
Sanak	links	0.268	0.0007	377.86***	Replicates	foodweb
Chaco	links	0.160	0.0260	6.17***	Islands	antagonistic
Gottin_pp	links	0.208	0.0242	8.59***	Islands	mutualistic
Gottin_hp	links	0.064	0.0504	1.27	Islands	mutualistic
Balbina	links	0.162	0.0894	1.81°	Islands	mutualistic
Bird.disp	links	0.449	0.1747	2.57*	Islands	mutualistic
Lakes	links	0.127	0.0230	5.51***	Islands	foodweb
Pyrenees	links	0.369	0.0128	28.75***	Biogeography	foodweb
Alpine	links	1.209	0.0032	378.06***	Biogeography	foodweb
Mediterranean	links	0.281	0.0005	528.86***	Biogeography	foodweb
Steppic	links	0.572	0.0031	184.62***	Biogeography	foodweb
Boreal	links	0.262	0.0003	860.01***	Biogeography	foodweb
Continental	links	0.490	0.0020	244.90***	Biogeography	foodweb
BlackSea	links	0.259	0.0031	82.26***	Biogeography	foodweb
Atlantic	links	0.444	0.0022	202.70***	Biogeography	foodweb
Arctic	links	1.061	0.0044	242.72***	Biogeography	foodweb
Pannonian	links	0.060	0.0007	90.85***	Biogeography	foodweb
Anatolian	links	0.230	0.0009	256.95***	Biogeography	foodweb
Salix1	links	0.267	0.0046	58.51***	Biogeography	antagonistic
Salix2	links	0.565	0.0036	154.88***	Biogeography	antagonistic

dataset	property	z-exponent	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	links/sp	0.174	0.0029	60.59***	Replicates	mutualistic
Garraf_pp	links/sp	0.144	0.0009	153.81***	Replicates	mutualistic
Montseny	links/sp	0.231	0.0020	116.15***	Replicates	mutualistic
Nahuel	links/sp	0.165	0.0029	57.39***	Replicates	mutualistic
Garraf_hp	links/sp	0.219	0.0027	79.89***	Replicates	antagonistic
Olot	links/sp	0.204	0.0033	61.74***	Replicates	antagonistic
Quecus	links/sp	0.188	0.0016	117.89***	Replicates	antagonistic
Soil1	links/sp	0.202	0.0022	93.45***	Replicates	foodweb
Soil2	links/sp	0.239	0.0029	81.91***	Replicates	foodweb
Soil3	links/sp	0.179	0.0014	125.88***	Replicates	foodweb
Soil4	links/sp	0.186	0.0017	110.66***	Replicates	foodweb
Soil5	links/sp	0.263	0.0050	52.30***	Replicates	foodweb
Soil6	links/sp	0.210	0.0020	105.50***	Replicates	foodweb
Soil7	links/sp	0.217	0.0019	111.21***	Replicates	foodweb
Bristol	links/sp	0.094	0.0017	55.13***	Replicates	foodweb
Sanak	links/sp	0.080	0.0004	219.42***	Replicates	foodweb
Chaco	links/sp	0.051	0.0130	3.93***	Islands	antagonistic
Gottin_pp	links/sp	0.073	0.0124	5.90***	Islands	mutualistic
Gottin_hp	links/sp	0.017	0.0199	0.89	Islands	mutualistic
Balbina	links/sp	0.034	0.0211	1.61	Islands	mutualistic
Bird.disp	links/sp	0.071	0.0200	3.56***	Islands	mutualistic
Lakes	links/sp	0.047	0.0126	3.76***	Islands	foodweb
Pyrenees	links/sp	0.144	0.0059	24.19***	Biogeography	foodweb
Alpine	links/sp	0.453	0.0021	213.95***	Biogeography	foodweb
Mediterranean	links/sp	0.130	0.0003	400.79***	Biogeography	foodweb
Steppic	links/sp	0.197	0.0012	169.22***	Biogeography	foodweb
Boreal	links/sp	0.095	0.0001	737.96***	Biogeography	foodweb
Continental	links/sp	0.167	0.0007	226.67***	Biogeography	foodweb
BlackSea	links/sp	0.136	0.0015	90.04***	Biogeography	foodweb
Atlantic	links/sp	0.175	0.0009	194.89***	Biogeography	foodweb
Arctic	links/sp	0.515	0.0025	207.90***	Biogeography	foodweb
Pannonian	links/sp	0.025	0.0004	58.88***	Biogeography	foodweb
Anatolian	links/sp	0.107	0.0004	250.70***	Biogeography	foodweb
Salix1	links/sp	0.078	0.0016	47.21***	Biogeography	antagonistic
Salix2	links/sp	0.276	0.0024	112.68***	Biogeography	antagonistic

dataset	property	z-exponent	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	indegree	0.327	0.0032	102.81***	Replicates	mutualistic
Garraf_pp	indegree	0.218	0.0015	148.23***	Replicates	mutualistic
Montseny	indegree	0.379	0.0039	96.60***	Replicates	mutualistic
Nahuel	indegree	0.210	0.0062	33.95***	Replicates	mutualistic
Garraf_hp	indegree	0.298	0.0037	79.61***	Replicates	antagonistic
Olot	indegree	0.524	0.0056	93.78***	Replicates	antagonistic
Quecus	indegree	0.068	0.0024	28.33***	Replicates	antagonistic
Soil1	indegree	0.202	0.0022	93.45***	Replicates	foodweb
Soil2	indegree	0.239	0.0029	81.91***	Replicates	foodweb
Soil3	indegree	0.179	0.0014	125.88***	Replicates	foodweb
Soil4	indegree	0.186	0.0017	110.66***	Replicates	foodweb
Soil5	indegree	0.263	0.0050	52.30***	Replicates	foodweb
Soil6	indegree	0.210	0.0020	105.50***	Replicates	foodweb
Soil7	indegree	0.217	0.0019	111.21***	Replicates	foodweb
Bristol	indegree	0.094	0.0017	55.13***	Replicates	foodweb
Sanak	indegree	0.043	0.0003	137.03***	Replicates	foodweb
Lakes	indegree	0.015	0.0254	0.59	Islands	foodweb
Chaco	indegree	0.051	0.0130	3.93**	Islands	antagonistic
Gottin_hp	indegree	-0.001	0.0397	-0.04	Islands	antagonistic
Gottin_pp	indegree	0.065	0.0262	2.49*	Islands	mutualistic
Bird.disp	indegree	0.158	0.0459	3.44**	Islands	mutualistic
Balbina	indegree	0.048	0.0398	1.21	Islands	mutualistic
Pyrenees	indegree	0.075	0.0047	15.96***	Biogeography	foodweb
Alpine	indegree	0.507	0.0028	182.64***	Biogeography	foodweb
Mediterranean	indegree	0.149	0.0003	472.85***	Biogeography	foodweb
Steppic	indegree	0.222	0.0015	148.99***	Biogeography	foodweb
Boreal	indegree	0.058	0.0002	313.09***	Biogeography	foodweb
Continental	indegree	0.202	0.0010	212.67***	Biogeography	foodweb
BlackSea	indegree	0.141	0.0014	97.65***	Biogeography	foodweb
Atlantic	indegree	0.148	0.0009	171.20***	Biogeography	foodweb
Arctic	indegree	0.358	0.0026	139.23***	Biogeography	foodweb
Pannonian	indegree	0.030	0.0005	56.15***	Biogeography	foodweb
Anatolian	indegree	0.123	0.0004	315.64***	Biogeography	foodweb
Salix1	indegree	0.129	0.0029	44.23***	Biogeography	antagonistic
Salix2	indegree	0.279	0.0045	61.28***	Biogeography	antagonistic

dataset	property	z-exponent	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	potential_indegree	-0.179	0.0011	-169.31***	Replicates	mutualistic
Garraf_pp	potential_indegree	-0.218	0.0013	-173.69***	Replicates	mutualistic
Montseny	potential_indegree	-0.250	0.0018	-135.97***	Replicates	mutualistic
Nahuel	potential_indegree	-0.199	0.0018	-113.50***	Replicates	mutualistic
Garraf_hp	potential_indegree	-0.216	0.0048	-45.07***	Replicates	antagonistic
Olot	potential_indegree	-0.175	0.0033	-52.55***	Replicates	antagonistic
Quecus	potential_indegree	-0.159	0.0014	-117.77***	Replicates	antagonistic
Soil1	potential_indegree	-0.014	0.0013	-10.64***	Replicates	foodweb
Soil2	potential_indegree	-0.007	0.0019	-3.78**	Replicates	foodweb
Soil3	potential_indegree	-0.034	0.0010	-32.84***	Replicates	foodweb
Soil4	potential_indegree	-0.041	0.0010	-43.51***	Replicates	foodweb
Soil5	potential_indegree	0.004	0.0022	1.90°	Replicates	foodweb
Soil6	potential_indegree	-0.067	0.0011	-63.12***	Replicates	foodweb
Soil7	potential_indegree	-0.016	0.0013	-12.49***	Replicates	foodweb
Bristol	potential_indegree	-0.095	0.0018	-52.83***	Replicates	foodweb
Sanak	potential_indegree	-0.075	0.0002	-352.23***	Replicates	foodweb
Gottin_hp	potential_indegree	-0.026	0.0237	-1.11	Islands	antagonistic
Chaco	potential_indegree	-0.037	0.0112	-3.27**	Islands	antagonistic
Gottin_pp	potential_indegree	-0.099	0.0219	-4.50**	Islands	mutualistic
Bird.disp	potential_indegree	0.031	0.0623	0.49	Islands	mutualistic
Balbina	potential_indegree	-0.049	0.0247	-1.99°	Islands	mutualistic
Lakes	potential_indegree	0.008	0.0132	0.57	Islands	foodweb
Alpine	potential_indegree	-0.029	0.0003	-90.36***	Biogeography	foodweb
Mediterranean	potential_indegree	-0.020	0.0001	-214.41***	Biogeography	foodweb
Pyrenees	potential_indegree	-0.112	0.0056	-20.05***	Biogeography	foodweb
Steppic	potential_indegree	-0.007	0.0002	-28.27***	Biogeography	foodweb
Boreal	potential_indegree	-0.071	0.0001	-486.31***	Biogeography	foodweb
Continental	potential_indegree	-0.015	0.0001	-139.41***	Biogeography	foodweb
BlackSea	potential_indegree	-0.016	0.0004	-37.44***	Biogeography	foodweb
Atlantic	potential_indegree	-0.050	0.0002	-282.73***	Biogeography	foodweb
Arctic	potential_indegree	-0.096	0.0021	-45.81***	Biogeography	foodweb
Pannonian	potential_indegree	0.001	0.0003	2.09*	Biogeography	foodweb
Anatolian	potential_indegree	0.003	0.0002	16.91***	Biogeography	foodweb
Salix1	potential_indegree	-0.042	0.0011	-36.61***	Biogeography	antagonistic
Salix2	potential_indegree	-0.265	0.0043	-61.80***	Biogeography	antagonistic

dataset	property	z-exponent	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	ratio	-0.158	0.0040	-39.68***	Replicates	mutualistic
Garraf_pp	ratio	0.199	0.0022	90.38***	Replicates	mutualistic
Montseny	ratio	-0.108	0.0062	-17.44***	Replicates	mutualistic
Nahuel	ratio	0.310	0.0053	58.83***	Replicates	mutualistic
Garraf_hp	ratio	0.092	0.0035	25.88***	Replicates	antagonistic
Olot	ratio	-0.251	0.0048	-51.97***	Replicates	antagonistic
Quecus	ratio	0.182	0.0029	62.95***	Replicates	antagonistic
Soil1	ratio	-0.029	0.0029	-10.22***	Replicates	foodweb
Soil2	ratio	0.020	0.0048	4.28***	Replicates	foodweb
Soil3	ratio	-0.021	0.0016	-13.18***	Replicates	foodweb
Soil4	ratio	-0.039	0.0019	-20.36***	Replicates	foodweb
Soil5	ratio	-0.038	0.0029	-12.92***	Replicates	foodweb
Soil6	ratio	0.040	0.0018	22.20***	Replicates	foodweb
Soil7	ratio	-0.004	0.0019	-2.14*	Replicates	foodweb
Bristol	ratio	0.114	0.0021	53.20***	Replicates	foodweb
Sanak	ratio	0.023	0.0004	65.87***	Replicates	foodweb
Lakes	ratio	0.018	0.0333	0.54	Islands	foodweb
Chaco	ratio	-0.007	0.0113	-0.64	Islands	antagonistic
Gottin_hp	ratio	0.036	0.0338	1.06	Islands	antagonistic
Gottin_Pp	ratio	0.057	0.0380	1.50	Islands	mutualistic
Bird.disp	ratio	0.122	0.2178	0.56	Islands	mutualistic
Balbina	ratio	0.012	0.0514	0.23	Islands	mutualistic
Pyrenees	ratio	0.062	0.0050	12.29***	Biogeography	foodweb
Alpine	ratio	-0.004	0.0005	-7.21***	Biogeography	foodweb
Mediterranean	ratio	-0.021	0.0001	-305.02***	Biogeography	foodweb
Steppic	ratio	-0.009	0.0002	-41.04***	Biogeography	foodweb
Boreal	ratio	0.033	0.0002	212.44***	Biogeography	foodweb
Continental	ratio	-0.016	0.0002	-103.05***	Biogeography	foodweb
BlackSea	ratio	-0.006	0.0003	-18.61***	Biogeography	foodweb
Atlantic	ratio	0.024	0.0002	130.67***	Biogeography	foodweb
Arctic	ratio	0.118	0.0017	69.97***	Biogeography	foodweb
Pannonian	ratio	-0.004	0.0002	-24.31***	Biogeography	foodweb
Anatolian	ratio	-0.019	0.0002	-81.38***	Biogeography	foodweb
Salix1	ratio	0.022	0.0055	3.98***	Biogeography	antagonistic
Salix2	ratio	0.211	0.0087	24.31***	Biogeography	antagonistic

dataset	property	z-exponent	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	modularity	-0.024	0.0028	-8.79***	Replicates	mutualistic
Garraf_pp	modularity	-0.061	0.0010	-60.34***	Replicates	mutualistic
Montseny	modularity	-0.162	0.0022	-74.59***	Replicates	mutualistic
Nahuel	modularity	-0.077	0.0027	-28.47***	Replicates	mutualistic
Garraf_hp	modularity	-0.084	0.0028	-30.17***	Replicates	antagonistic
Olot	modularity	-0.085	0.0031	-27.04***	Replicates	antagonistic
Quecus	modularity	-0.104	0.0017	-63.20***	Replicates	antagonistic
Soil1	modularity	-0.030	0.0110	-2.77**	Replicates	foodweb
Soil2	modularity	-0.012	0.0340	-0.36	Replicates	foodweb
Soil3	modularity	0.161	0.0188	8.57	Replicates	foodweb
Soil4	modularity	-0.469	0.0617	-7.60***	Replicates	foodweb
Soil5	modularity	-0.273	0.0805	-3.39***	Replicates	foodweb
Soil6	modularity	-0.750	0.0527	-14.22***	Replicates	foodweb
Soil7	modularity	-0.802	0.0595	-13.48***	Replicates	foodweb
Bristol	modularity	0.103	0.0063	16.52***	Replicates	foodweb
Sanak	modularity	-0.013	0.0011	-12.21***	Replicates	foodweb
Lakes	modularity	0.077	0.0444	1.74	Islands	foodweb
Chaco	modularity	-0.041	0.0126	-3.25**	Islands	antagonistic
Gottin_hp	modularity	0.023	0.0191	1.23	Islands	antagonistic
Gottin_pp	modularity	0.022	0.0193	1.13	Islands	mutualistic
Bird.disp	modularity	-0.049	0.0540	-0.91	Islands	mutualistic
Balbina	modularity	-0.094	0.0717	-1.32	Islands	mutualistic
Pyrenees	modularity	-0.001	0.0197	-0.04	Biogeography	foodweb
Alpine	modularity	-0.256	0.0051	-50.29***	Biogeography	foodweb
Mediterranean	modularity	-0.043	0.0003	-129.90***	Biogeography	foodweb
Steppic	modularity	-0.099	0.0006	-156.52***	Biogeography	foodweb
Boreal	modularity	-0.248	0.0029	-86.24***	Biogeography	foodweb
Continental	modularity	-0.091	0.0004	-237.79***	Biogeography	foodweb
BlackSea	modularity	-0.120	0.0020	-59.64***	Biogeography	foodweb
Atlantic	modularity	-0.111	0.0088	-12.66***	Biogeography	foodweb
Pannonian	modularity	-0.027	0.0005	-56.49***	Biogeography	foodweb
Anatolian	modularity	-0.119	0.0033	-35.96***	Biogeography	foodweb
Salix1	modularity	-0.017	0.0015	-11.27***	Biogeography	antagonistic
Salix2	modularity	-0.075	0.0042	-17.85***	Biogeography	antagonistic

Appendix S3.3. Pairwise comparison results for interaction types. Comparisons between interaction types using Wilcoxon rank sum test of the z-exponents of the power relationships (in order): species-area, links-area, links/species-area, links-species, indegree-area, potential indegree-area. ‘Mut.’ corresponds to mutualistic interactions; ‘Ant.’ to antagonistic interactions; ‘Food.’ correspond to food webs.

	z SAR		z LAR		z L.SAR		z L-S		z Indegree		z Potential	
	Mut.	Ant.	Mut.	Ant.	Mut.	Ant.	Mut.	Ant.	Mut.	Ant.	Mut.	Ant.
Food.	0.33	0.33	0.53	0.80	0.73	0.93	<0.001	0.03	1	1	0.025	0.025
Ant.	0.59	/	0.82		0.73	/	0.16	/	1	/	0.710	/

Appendix S3.4. Power function fit for for the links-species relationship for each dataset. P-value significance is shown by: ° < 0.1, * < 0.05, ** < 0.01, *** < 0.001. We used nonlinear least squares (NLS) with the 'nls' function in R.

dataset	property	Estimate	Std..Error	t.value	data_type	interaction_type
Garraf_pp2	links	1.555	0.0084	184.04***	Replicates	mutualistic
Garraf_pp	links	1.236	0.0021	600.88***	Replicates	mutualistic
Montseny	links	1.510	0.0045	333.51***	Replicates	mutualistic
Nahuel	links	1.312	0.0076	173.76***	Replicates	mutualistic
Garraf_hp	links	1.423	0.0067	212.29***	Replicates	antagonistic
Olot	links	1.455	0.0120	121.51***	Replicates	antagonistic
Quecus	links	1.619	0.0070	232.39***	Replicates	antagonistic
Soil1	links	1.770	0.0070	253.39***	Replicates	foodweb
Soil2	links	1.810	0.0088	206.84***	Replicates	foodweb
Soil3	links	1.698	0.0045	377.86***	Replicates	foodweb
Soil4	links	1.726	0.0048	360.43***	Replicates	foodweb
Soil5	links	1.769	0.0086	205.38***	Replicates	foodweb
Soil6	links	1.873	0.0067	278.82***	Replicates	foodweb
Soil7	links	1.790	0.0052	343.29***	Replicates	foodweb
Bristol	links	1.697	0.0118	144.09***	Replicates	foodweb
Sanak	links	1.342	0.0018	749.63***	Replicates	foodweb
Lakes	links	1.369	0.0663	20.63***	Islands	foodweb
Chaco	links	1.394	0.1051	13.26***	Islands	antagonistic
Gottin_hp	links	1.268	0.0858	14.78***	Islands	antagonistic
Gottin_pp	links	1.320	0.0836	15.79***	Islands	mutualistic
Bird.disp	links	1.301	0.0399	32.57***	Islands	mutualistic
Balbina	links	1.211	0.0674	17.99***	Islands	mutualistic
Pyrenees	links	1.586	0.0188	84.46***	Biogeography	foodweb
Alpine	links	1.968	0.0021	941.35***	Biogeography	foodweb
Mediterranean	links	1.800	0.0014	1269.26***	Biogeography	foodweb
Steppic	links	1.981	0.0012	1669.36***	Biogeography	foodweb
Boreal	links	1.613	0.0004	4064.64***	Biogeography	foodweb
Continental	links	1.947	0.0010	1994.67***	Biogeography	foodweb
BlackSea	links	1.908	0.0034	557.06***	Biogeography	foodweb
Atlantic	links	1.947	0.0019	1012.57***	Biogeography	foodweb
Arctic	links	1.548	0.0014	1101.58***	Biogeography	foodweb
Pannonian	links	1.826	0.0097	188.43***	Biogeography	foodweb
Anatolian	links	1.878	0.0028	660.36***	Biogeography	foodweb
Salix1	links	1.321	0.0062	213.21***	Biogeography	antagonistic
Salix2	links	1.962	0.0128	152.78***	Biogeography	antagonistic

Chapter 4

GEOGRAPHICAL VARIATION OF THE SPATIAL SCALING OF NETWORK STRUCTURE

4.1 TITLE OF THE SCIENTIFIC ARTICLE:

*The spatial scaling of network structure across European biogeographical regions*⁵

ABSTRACT

Aim: The species-area relationship (SAR) has been one of the most fundamental properties in ecology. Yet, ecological communities are not only constituted by the species present in a region but also by the interactions between them. Whether the structure of the complex network of interactions changes with area size and which are the main mechanisms affecting these changes, is still largely unknown. Here, we analysed the spatial scaling of network structure across Europe and asked whether there is geographical variation in the specific shape of the network-area relationships (NARs), what are the main environmental determinants of the variation observed between biogeographical regions and what is the contribution of species richness for the patterns observed.

Location: Europe.

Time period: Present.

Major taxa studied: Terrestrial vertebrates.

Methods: We combined species distribution maps for all European terrestrial vertebrate species and an expert-based metaweb (1141 species and 69,724 links) with all potential interactions, to determine the terrestrial vertebrate assemblage at each 10km cell within Europe. We then considered ten biogeographical regions in Europe and analysed how network structure scales with increasing area size in each of them. At each spatial scale, we analysed eight different network metrics reflecting the complexity (i.e., number of species and links, and number of links per species, mean generality and vulnerability) and vertical diversity (i.e., proportion of species per trophic level) of the resulting ecological communities. We then analysed the contribution of species richness and the main environmental determinants for the differences observed in the spatial scaling of the different biogeographical regions.

Results: The spatial scaling of network complexity strongly varied across biogeographical regions. However, once variation in the spatial scaling of species richness across Europe was accounted for, differences in the shape of the NARs disappeared. Instead, network vertical diversity remained remarkably stable across biogeographical regions and across spatial scales, despite the great variation in species richness. The spatial variation in the mean annual temperature and the spatial clustering of habitats showed to be the main determinants of the shape of SARs across Europe.

Main conclusions: Species richness emerges as a faithful predictor of network complexity but not of network vertical diversity. The universalities found in the proportion of species across trophic levels indicate that ecological communities preserve basic structural properties that are scale invariant which might be beneficial for their persistence and stability.

⁵ This chapter represents a collaboration with Miguel Lurgi, Joao Braga, Ceres Barros, Luigi Maiorano, Francesco Ficetola, Wilfried Thuiller and José M. Montoya. In preparation to submit to *Global Ecology and Biogeography*.

4.2 INTRODUCTION

One of the most fundamental patterns in ecology is the increase of the total number of species as the area sampled increases [79], [81], [83]. The species-area relationship (SAR) has been established as a fundamental property of biological systems [82], [83] and an important tool for the disciplines of conservation biology and landscape ecology [178]–[180]. Yet, ecological communities are composed not only of the collection of species co-occurring in space, but also of interactions connecting them – the so-called species interaction network. Biological diversity should be thus measured in terms of both species and their biotic interactions.

Biotic interactions affect species' spatial distributions through several mechanisms, such as inhibition (e.g., in trophic or competitive interactions) or facilitation (e.g., in mutualistic or commensalistic interactions), at every spatial scale [36], [243], [244]. Furthermore, recent studies also suggest that they can influence species responses to environmental perturbations, like climate change or biological invasions [158], [217], [245]. Habitat destruction and fragmentation have been shown to not only affect species richness, but also the diversity and structure of their trophic interactions [2], [207], [209]. The study of the spatial scaling of biodiversity should thus, not only account for the changes in species richness but also interaction network structure [103], [109], [242].

Several factors have been proposed to explain the variation found in the strength and slope of SARs [94], [219]. These include, but are not limited to: the spatial scale of observation [94], [219], [246], [247], the taxonomic group or the species trophic rank considered [248], [249] and environmental factors, such as geographical gradients [94], [248] or the habitat heterogeneity of the region [94], [250]–[252]. In contrast, research on the possible mechanisms affecting the spatial scaling of network structure has just started. Different theoretical approaches have suggested possible mechanisms affecting the variation of network structure across spatial scales [86], [109], [242], [253]. In chapter 2 [124], I presented a theoretical framework that predicts the existence of a number of network-area relationships (NARs) arising from different spatial mechanisms and assembly processes. The main mechanisms proposed are the existence of different SARs across trophic levels, the preferential selection of generalist species at small spatial extents and the effect of dispersal limitation promoting beta-diversity. Empirical approaches are, however, missing. One exception to this lack of empirical knowledge, together with the work developed in chapter 3, is the work by Wood and colleagues [103], where the authors analysed the effects of spatial scale when sampling marine intertidal food webs in Alaska. They found that most of the changes observed in food web structure across spatial scales were controlled by changes in species richness and food web connectance.

It is empirically well-supported, and properly understood theoretically, that many aspects of network structure change systematically with changes in food web species diversity and connectance [99], [100], [102], [150], [254]. An increase in species richness will necessarily generate an increase in the number of links that will further alter the connectivity of the food web depending on the scaling of the number of links with species richness (see [104], [107], [108]). Moreover, at equal number of species, networks with different connectances are expected to have different degree distributions [150]. Comparative studies addressing the variation in network properties must, therefore, account for the effect of changes in species richness and connectance on the rest of the food web properties. This is particularly relevant in studies where a gradient in diversity exists, such as biogeographical studies, because of the latitudinal gradient in species richness [151], [152], or studies addressing multiple spatial scales, because of the spatial scaling in diversity [79], [81], [83].

Empirically documenting network structure across spatial scales, can be extremely costly and time-consuming [112]. Especially so if one attempts to analyse vast ranges of spatial extents, like it has been done for SARs. Instead of solely relying on observed interactions, the occurrence of biotic interactions can also be inferred from known and expert knowledge on who eats whom, coupled with measurable information on species distributions, species traits and environmental conditions. The use of potential networks or 'metawebs' (*sensu* Dunne [5]) is thus rising due to the increasing amount of high quality data available and the development of new analytical tools that allow to better predict the presence/absence of interactions [112]–[115]. This diversification of tools to assemble ecological communities together with increasingly powerful predictive models for species distributions, opens new avenues to analyse and quantify network structure at large biogeographical scales.

Here we use the potential food web of European terrestrial vertebrate species, and their continental distribution, to determine: 1) whether different aspects of network structure are equally affected by area size, 2) whether there is geographical variation across Europe in the spatial scaling of network structure, 3) what are the main environmental determinants of the variation among biogeographical regions and 4) what is the contribution of species richness to the patterns observed in NARs. We combined species distribution maps for all terrestrial vertebrate species in Europe and an expert-based metaweb with all their potential trophic interactions to determine the structure of local food webs at each 10 x 10 Km pixel within Europe. We then considered ten European bio-geographical regions and analysed the spatial scaling of network structure in each of them. We analysed eight different network metrics reflecting the complexity (i.e., number of species, links and links per species, mean generality and vulnerability) and the vertical diversity (i.e., proportion of species per trophic level) of the

resulting ecological communities. We additionally analysed the contribution of species richness for the patterns observed and the main environmental determinants of the differences in the shape of SARs across Europe.

4.3 METHODS

We built network-area relationships (NARs) (*sensu* [124]) by quantifying measures of food web structure at different spatial scales, from local to regional. We used two sources of information to infer trophic links between species: (i) species presence at the spatial scale analysed (based on species distribution maps), and (ii) the existence of a trophic interaction between pairs of species in the metaweb (i.e. the network of all potential interactions between species in Europe). We then determined specific NARs for different biogeographical regions in Europe and compared their shapes. We analysed the relationships between all network metrics with species richness, and we finally analysed the environmental and spatial factors determining the shape of SARs across biogeographical regions.

4.3.1 Study area and species distributions

The study area comprises the entire European sub-continent, except Macaronesia. Portugal and Iceland are the southernmost and northernmost westward limits, respectively, and the Ural Mountains are the easternmost limit (Figure 1). The region is limited by Fennoscandia in the north, and the Mediterranean coast in the south. Turkey, geographically part of Asia, was also included to provide a complete picture of the Mediterranean coast [255]. We refer to this area as Europe. Species distribution maps were obtained from a previous study by Maiorano et al. (2013), who estimated them from expert-based distribution models in which species presence was filtered by habitat preferences across their known distribution. Their method relied on georeferenced presence data points of terrestrial vertebrate species across Europe, extracted from digital repositories, and expert knowledge on the habitat requirements and environmental factors most likely limiting the distribution of all the terrestrial vertebrate species for which they had records in Europe. Thus, distribution estimates incorporating information on habitat suitability, elevation range and distance to water (the main variables identified by the authors as relevant for inferring these species' distributions) yielded maps at 300m resolution for 510 species of breeding birds, 288 mammals, 239 reptiles, and 103 amphibian species, which together conform our species database. A full account of the methodology used to obtain the distribution maps, including all the sources of data can be found in [255]. We up-scaled all species range maps to a 10 Km resolution by considering a species to be present on a given 10 x 10 Km cell if it was present in at least one of the 300 x 300 m cells within it. This upscaling procedure was performed to: 1) facilitate the

expression of the effects of habitat heterogeneity on network structure at different spatial scales, and 2) because presence data was coarser for many of the species studied species (e.g., 50Km), with 10Km cell sizes representing a good compromise between the largest and smallest species.

4.3.2 European terrestrial vertebrate metaweb

Trophic interactions between all species in the database were estimated based on literature reviews and expert knowledge. A trophic interaction was considered feasible between any pair of species when one of the species potentially preys on any life stage of another species (e.g., egg and larval when applicable, juvenile or adult). Trophic interactions between a predator and a prey were identified from published accounts of their observation, morphological similarities between potential prey and literature-referenced prey and, in the few cases where this information was absent, the diet of the predator's sister species. Sister species were defined as the closest genus-level relative found in the dataset. The inferred interactions thus comprised all potential interactions between terrestrial vertebrate species in the European region. Note that interactions specified in this way may not be realised in all locations or time periods.

4.3.3 Local assemblages and food web properties

Local assemblages were built by intersecting the metaweb information with the distribution maps of the species. Thus, for each 10 x 10 Km cell in the map, we considered all species present and determined the interactions between them using the information provided by the metaweb. If a given species was present in a cell, but had no available prey or did not share a common habitat type with any of its prey, the species was considered absent in that particular location (i.e., we assume a false positive in the distribution data; [86]). Once we built food webs using the criteria outlined above, we analysed their structure by quantifying several network properties that are commonly used in the literature to study food webs [256]. We classified these properties into two broad categories: complexity and vertical diversity.

To quantify food web complexity, we measured: number of species (S), number of links (L), links per species (L/S), mean vulnerability (the average number of predators per prey species; $(\sum_{S_i \text{ in } S_{prey}} Pred(S_i)) / S_{prey}$), and mean generality (the average number of prey items per predator; $(\sum_{S_i \text{ in } S_{pr}} Pr(S_i)) / S_{pr}$). Vertical diversity, on the other hand, was quantified by measuring the fraction of basal (B), intermediate (I) and top (T) species (i.e., species without prey, with both prey and predators,

and without predators, respectively). It is important to note that basal species in this case are not in fact basal resources (i.e., primary producers), as it is the case in most food web studies. In the food webs presented here, the fraction of basal resources (B) refers to the vertebrate species in our data set which do not have resources. Additionally, network modularity (M) was quantified using the modularity function (Q) proposed by Newman and Girman [225]:

$$Q = \frac{1}{2m} \sum_{i,j} (A_{ij} - P_{ij}) \delta(g_i, g_j)$$

where m is the number of edges in the network, A_{ij} are the adjacency matrix elements (1 if a link between vertices i and j exists and 0 otherwise), P_{ij} is the expected number of links between i and j (i.e., $k_i k_j / 2m$, with k the degree of a vertex), g_i is the compartment to which vertex i belongs (as described in [226]). $\delta(r, s) = 1$ if $r = s$ and 0 otherwise. We used the random-walk based algorithm walktrap [227] implemented in the R package *igraph* [228]. Table 4 shows all the properties for the metaweb

Table 4. Metaweb properties. Network complexity metrics: number of species, links, links per species, connectance, mean indegree and mean outdegree. Vertical diversity metrics: proportion of basal, intermediate and top species and percentage of omnivorous links. Network modularity indicates the presence of densely linked groups within the network.

Property	Value
Number of Species	1140
Connectance	0.054
Number of Links	69724
Links/Species	561.107
Indegree	183.96
Outdegree	61.21
Proportion of Basal	0.68
Proportion of Intermediate	0.31
Proportion of Top	0.02
Omnivory	0.99
Modularity	0.24

4.3.4 Building network-area relationships

The three elements described above: species distributions maps, the metaweb, and food web properties allowed us to build network-area relationships. We call network-area relationships (NARs) the changes in food web properties as area size increases. The spatial resolution of the species distribution maps (i.e., 10 x 10 Km) determines the local scales of our study. To simulate a spatial scale continuum we

iteratively aggregated map cells, one by one, into larger areas of different sizes (see detailed explanation of the aggregation procedure below). This allows sampling the study area at different spatial scales. Once sampling areas were defined, we constructed food webs at each spatial scale using the information on species presence/absence for each aggregation of map cells and extracting from the metaweb the corresponding trophic interactions between the species present. Because food webs constructed thus might contain interactions between species that do not necessarily occur across the whole area of a grid cell, food web structure at large spatial scales must be understood as the structure of the potential network of interactions at a given area. Lastly, we calculated the food web properties identified above for each of these food webs. This allowed us to lay out the relationships between area size (i.e., number of map cells) and network properties: the NARs.

4.3.5 Spatial aggregation

To simulate a continuum of spatial scales we aggregated map cells to increase the area sampled starting from cell sizes equal to the resolution of the species distribution maps (i.e., local communities). There are several ways in which map cells can be aggregated to consider larger spatial extents, such as a random aggregation of cells, or a linear aggregation based on nearest neighbours. Because ecological communities in nature are most likely comprised of assemblages of species that live geographically close to each other, we developed an algorithm for cell aggregation that allows ensuring spatially coherent communities at different scales. Starting from a randomly chosen cell, our algorithm aggregates cells by choosing neighbouring ones in a 'spiral', ever-increasing way from the local (i.e., one 10 x 10 Km cell) to the desired spatial scale. The largest (i.e., regional) spatial scale comprises the aggregation of all the cells in the map. Since the starting point of this aggregation procedure is randomly chosen, species composition of communities is dependent on the geographical location of this starting point. Hence, we performed 100 replicated aggregations starting from different random locations on the map to account for the variability arising from the choice of the starting point of aggregation (i.e., the first cell). This produced 100 replicated NARs for each of the biogeographical regions considered (see below).

4.3.6 Biogeographical regions

To look at the differences in the scaling of biodiversity across gradients of ecological and environmental factors, we built unique SARs and NARs for different biogeographical regions in Europe (Figure 26). The European Environmental Agency (EEA) has defined a zonation of Europe into 'bioregions', based on similarities in environmental and habitat conditions across these geographical areas. We obtained geographical boundaries of these bioregions from the EEA (<https://www.eea.europa.eu/data->

and-maps/data/biogeographical-regions-europe-3). We used 10 European biogeographical regions from this classification: Alpine, Anatolian, Arctic, Atlantic, Black Sea, Boreal, Continental, Mediterranean, Pannonian and Steppic. We removed the Macaronesian region from our analyses because of the large discrepancy in size with the rest of the bioregions analysed. A full description of each biogeographical region is freely available online in the EEA webpage (www.eea.europa.eu).

Individual maps for each bioregion were overlaid on the species distribution maps using the *rgdal* package (see Study area and species distributions section) to determine the bioregion membership of each cell of the map, and in turn determine the distribution of each species on each bioregion. This allowed us to build NARs independently for each bioregion using the methodology outlined above, considering the metaweb as unique across Europe.

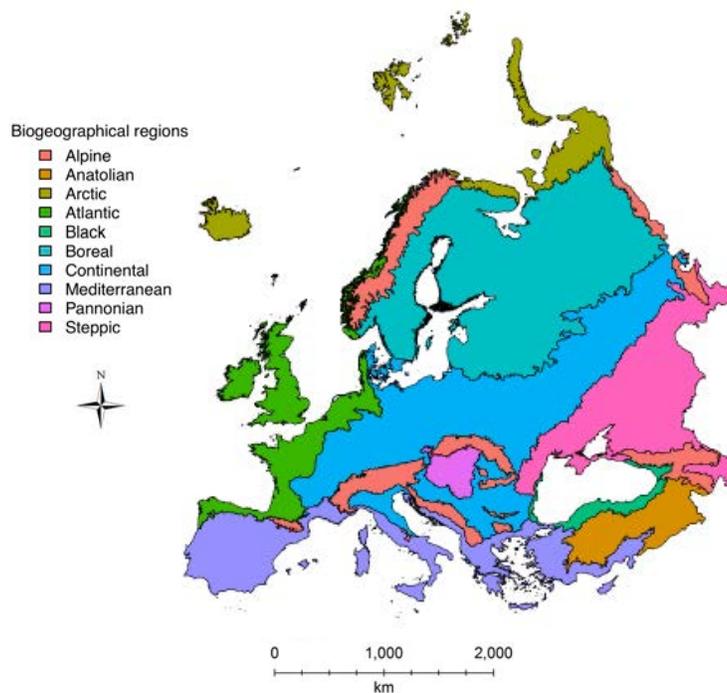


Figure 26. Study area. Biogeographical regions in Europe as defined by the European Environmental Agency (<https://www.eea.europa.eu/data-and-maps/data/>; accessed on June 2018).

4.3.7 Spatial and environmental variables

To assess whether differences in the shape of SARs and NARs across bioregions were related to their environmental features, we characterised bioregions according to a set of variables quantifying different aspects of their environmental features and spatial complexity. The spatial and environmental variables considered were: (i) the average and the (ii) standard deviation of the annual mean temperature across cells, (iii) the average and the (iv) standard deviation of temperature seasonality across cells, (v)

the dissimilarity (Bray-Curtis) and (vi) spatial clustering (Moran's I) of habitat composition, (vii) the total area of the bioregion and (viii) the total number of habitats contained in each bioregion.

To be able to quantify the environmental variables for each biogeographical region, we used three measures at the cell level: (a) habitat composition, (b) annual mean temperature, and (c) temperature seasonality (a measure of the variability of temperature throughout the year). The map of habitat composition was obtained from data on land cover from GlobCover V2.2 (http://due.esrin.esa.int/page_globcover.php). Data from GlobCover comprises 46 land-use/land-cover classes at the European level. We calculated the proportion of each land cover class at a 300 m resolution within every single 10 km cell. For each cell, we then calculated habitat heterogeneity based on the land cover composition of the 300 m cells comprising them.

Habitat spatial structure within each bioregion was quantified using measures of habitat diversity and spatial clustering. Habitat diversity was quantified using the Bray-Curtis dissimilarity index. Bray-Curtis quantifies the dissimilarity between two sites (map cells in our case) based on the abundance of unique species (habitats in our case) found in each site:

$$BC_{ij} = 1 - \frac{2 C_{ij}}{S_i + S_j}$$

where C_{ij} is the sum of the lesser values for only those habitats in common between both cells. S_i and S_j are the total number of habitat units (see above) counted at both cells. Bray-Curtis indexes were calculated for all cell pairs in each bioregion using the *vegdist* function in the *vegan* [257] package, and then averaged per bioregion.

Habitat clustering, a measure of the degree to which cells of the same habitat are clustered together within each bioregion, was quantified for each bioregion independently at a 10 x 10 Km cell resolution. Ecologically, this measure corresponds to the extent to which a species perceives the habitat being homogeneous at local scales. To quantify habitat clustering we used the Moran's I index of spatial autocorrelation. This index ranges from -1 (total spatial decorrelation) to +1 (total autocorrelation). Thus, Moran's I values close to -1 for a given habitat indicate that it is very sparse across its range, while habitats for which values of Moran's I close to +1 are observed exhibit high spatial coherence. Moran's I is calculated using the following formula:

$$I = \frac{N}{W} \frac{\sum_i \sum_j \omega_{ij} (x_i - \bar{x})(x_j - \bar{x})}{\sum_i (x_i - \bar{x})^2}$$

where N is the number of cells in the bioregion being considered, indexed by subscripts i and j ; $x = 1$ if the habitat is present in the corresponding cell and 0 otherwise; \bar{x} is the mean of x (i.e., the fraction of cells harbouring that habitat); ω_{ij} are elements of a matrix of spatial weights with zeros on the diagonal and 1 if cell i is a directly adjacent neighbour of cell j ; and W is the sum of all ω_{ij} . We used the *raster* package to calculate Moran's I for each habitat within each bioregion, and the average value across habitats was calculated per bioregion.

Bioclimatic data (i.e., annual mean temperature and temperature seasonality) were obtained from WORLDCLIM [258] using the *raster* package in *R* [259] at a 10 x 10 Km resolution to match the species distribution maps. Mean and standard deviation of the climatic variables were extracted for each bioregion.

4.3.8 Statistical analyses

NARs shapes were statistically quantified by fitting power functions to the relationships obtained between network properties and area size using nonlinear least squares (NLS) regression with the *nls* function. As previously observed in chapter 2, we observed linear relationships between food web properties and the number of species in the web. To quantify the contribution of species richness to the variability of the spatial scaling of those properties, we performed linear correlations between them. Given that all food web complexity measures were highly correlated with species richness, we used the differences between SARs to determine the role of different environmental factors on the spatial scaling of ecological communities. Specifically, we used the exponents obtained with the fit of the power functions to SAR in each biogeographical region instead of using the scaling exponents of each network complexity property because they provided redundant information. Because the proportion of species per trophic level did not significantly vary across spatial scales or across biogeographical regions, we did not perform the test to determine the role of the environmental factors on them.

Therefore, habitat spatial structure and environmental variables were tested as predictors for the shape of the scaling of SARs. Pearson correlation coefficients were used to quantify the relationship between the predictor variables with the aim of detecting potential sources of multicollinearity. To avoid the problems inherent to multicollinearity of predictor variables we used commonality analysis [260], [261] to evaluate the relative contribution of each variable to the predictive power of a linear regression model incorporating the predictor variables described above. Unique vs. common contribution to model explanatory power, and variable inflation factors were used to select the set of variables that better explained variability in the models. The selected predictors were used in linear regressions to test their

effects and significance on explaining the scaling of SARs across biogeographical regions (see Appendix S4.1 for further details on the commonality analyses used). All analyses were performed in R (R Core Team 2017).

4.4 RESULTS

4.4.1 Network-Area Relationships

The spatial scaling of most network properties varied across biogeographical regions in Europe (Figure 27; Appendix S4.2). All network complexity metrics (i.e., number of species, links, links/species, mean generality and mean vulnerability) increased with area size. However, the scaling exponent (z) of each network property with area differed between biogeographical regions (Appendix S4.2). The z -exponents of the number of species with area ranged from 0.08 (Pannonian) to 0.38 (Alpine). A universal pattern emerged in the way the different complexity metrics scaled with area. For most biogeographical regions, while the number of links per species, mean generality and mean vulnerability scaled with area at the same rate as the number of species (i.e., very similar z of the fitted power functions), the number of links scaled twice as fast. That is, the scaling exponents of the number of links with area ranged between 0.16 and 0.77 (Appendix S4.2), meaning that communities were gaining more links than species as area increased. Exceptions for this pattern were Arctic and Boreal regions, which showed a scaling in the number of links ($z=0.46$ and $z=0.25$, respectively) closer to that observed for the number of species ($z=0.31$ and $z=0.15$), effectively slowing down the scaling of the other complexity properties with area (Figure 27).

In contrast, vertical diversity properties, specifically the proportion of species per trophic level, were largely scale-invariant. The proportion of basal, intermediate and top species showed similar values from local to regional spatial scales, and across biogeographical regions, including at the metaweb level (i.e., at the European level without considering biogeographical regions) (Figure 28, Table 5). The Arctic biome was an exception, showing a higher proportion of basal and top species (0.71 and 0.07, respectively), and lower proportion of intermediate species (0.21) than remaining bioregions. It also showed the largest variation in the proportions across spatial scales (Figure 28; Table 5). It is important to notice that the proportion of top species is very low due to the potential nature of our metaweb. That is, given that the metaweb is composed by all potential links between species, it is difficult to find a species having no potential predators, which constitutes the defining feature of a top species. Therefore, the proportion of top species might be reduced by the potentiality of the metaweb, while the proportion of intermediate species might be enlarged.

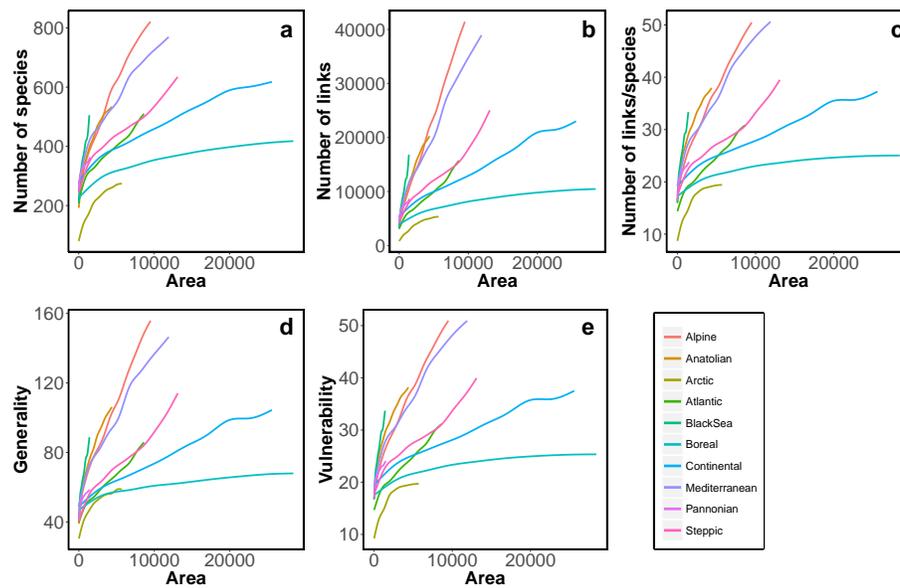


Figure 27. The spatial scaling of network complexity metrics across biogeographical regions in Europe. For a detailed description of the network properties see methods. Notice that total area and maximum values of network properties differ among biogeographical regions increasing the visual differences between them. Lines represent a generalized additive model fit to data points.

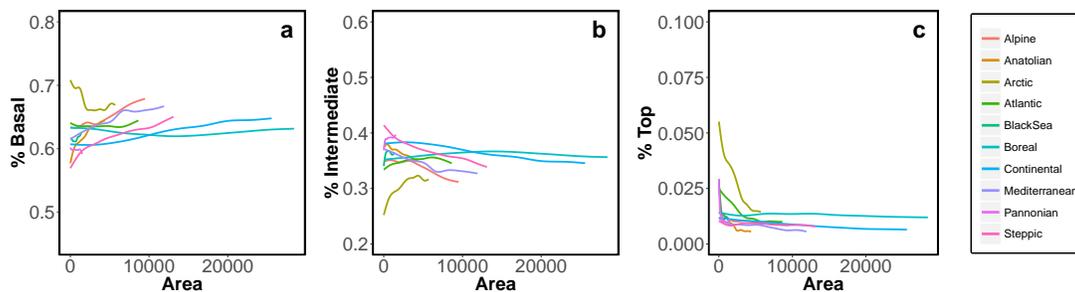


Figure 28. Relationship of the percentage of (a) basal, (b) intermediate and (c) top species with area across biogeographical regions in Europe. For a detailed description of each trophic level see methods. Lines represent a generalized additive model fit to data points.

Table 5. Proportion of species in each trophic level at local and regional spatial scales across the biogeographical regions in Europe. Local scale corresponds to the average proportion of species in each trophic level across all 10km² cells from each region. Regional scale corresponds to the network resulting from the aggregation of all the cells from each biogeographical region. The Metaweb corresponds to the whole Europe without considering biogeographical regions.

	% Basal		% Intermediate		% Top				
	Local	Regional	Local	Regional	Local	Regional			
Metaweb	0.63	0.06	0.71	0.33	0.06	0.28	0.04	0.03	0.05
Alpine	0.63	0.03	0.68	0.34	0.04	0.31	0.02	0.01	0.008
Arctic	0.71	0.07	0.67	0.21	0.07	0.31	0.07	0.04	0.014
Atlantic	0.64	0.02	0.65	0.32	0.03	0.34	0.03	0.02	0.001
BlackSea	0.61	0.03	0.63	0.34	0.04	0.36	0.03	0.02	0.01
Boreal	0.64	0.03	0.63	0.35	0.03	0.36	0.02	0.01	0.01
Continental	0.62	0.02	0.65	0.36	0.03	0.35	0.02	0.01	0.006
Mediterranean	0.61	0.04	0.68	0.36	0.04	0.32	0.02	0.02	0.005
Pannonian	0.61	0.02	0.59	0.36	0.02	0.39	0.03	0.01	0.01
Steppic	0.56	0.03	0.65	0.41	0.04	0.34	0.02	0.02	0.007
Anatolian	0.56	0.03	0.64	0.35	0.05	0.31	0.02	0.01	0.008

4.4.2 Contribution of species richness to NARs

To determine the contribution of the spatial scaling of species richness to the scaling of the remaining network properties, we analysed the correlation of each property with species richness for each biogeographical region (Figure 29; Appendix S4.3). All network complexity properties were highly correlated with species richness in all biogeographical regions (Figure 29a-d), with a mean adjusted-R² = 0.97 0.03, across all measures of complexity and biogeographical regions (Appendix S4.3). Importantly, the slopes of the relationships were remarkably similar, removing thus all differences between regions and between replicates. In all regions, the mean number of prey per predator (i.e., mean generality) increased with species richness much faster than the number of links per species and the mean number of predators per prey (i.e., mean vulnerability), indicating that the increase in species richness is faster at the lower trophic levels of the network (Appendix S4.3; Appendix S4.4). That is, as species richness increases, the accumulation of basal species is larger than the accumulation of intermediate and top species. Top predators actually do not increase in numbers with increasing species richness (Appendix S4.4). Interestingly, the number of links scaled exponentially with species richness (slope = 1.88 0.14; Figure 29a; Appendix S4.3) in all biogeographical regions.

In contrast, the proportion of species per trophic level did not show high correlations with the number of species for most biogeographical regions (mean adjusted- $R^2 = 0.39$ 0.27). The estimated slope of the relationships was extremely close to 0, indicating that the proportion of species per trophic level does not change significantly as total species richness increases (Figure 29e-g; Appendix S4.3). Therefore, food web complexity in the European terrestrial vertebrate assemblage correlated strongly with the number of species while its vertical diversity showed to be invariable across spatial scales, network richness and biogeographical regions.

4.4.3 Main drivers of Species-Area relationships

Given that species richness seemed to be the main determinant of the differences observed in the spatial scaling of network complexity across the biogeographical regions in Europe, we analysed potential environmental factors affecting the scaling of species richness with area within each region (Appendix S4.5). Analysis of the correlation between predictor variables indicated a potential for high degree of collinearity between them (Appendix S4.5), which would bias the results obtained from classical statistical models. Commonality analysis revealed that, among the predictor variables considered, only the standard deviation of the mean annual temperature across cells in each region and the spatial clustering of habitats (i.e. Moran's Index), were robust predictors of the scaling exponent (z) of the SAR (Appendix S4.1), after accounting for variance common contributions and inflation factors of the rest of the variables. Together, the spatial variation in the mean annual temperature and the spatial clustering of habitats within each biogeographical region, explained 85.53% (p -values = 0.001 and 0.093, respectively) of the variability observed in the exponents of SARs across Europe. Therefore, regions with larger spatial variability in their mean annual temperature and higher habitat clustering (i.e., more continuous habitat patches), tended to accumulate species faster as area sampled increased, which in turn affected the spatial scaling of network structure. The Arctic has the highest spatial variability in the mean annual temperature and, therefore, the fastest accumulation of species with area, followed by Alpine regions which showed the highest clustering of habitats in space. For both environmental variables, the Pannonian region showed the smallest values (i.e., less habitat clustering and less spatial variability in the mean annual temperature), which resulted in the slowest accumulation of species with area (Appendix S4.2 and Appendix S4.5).

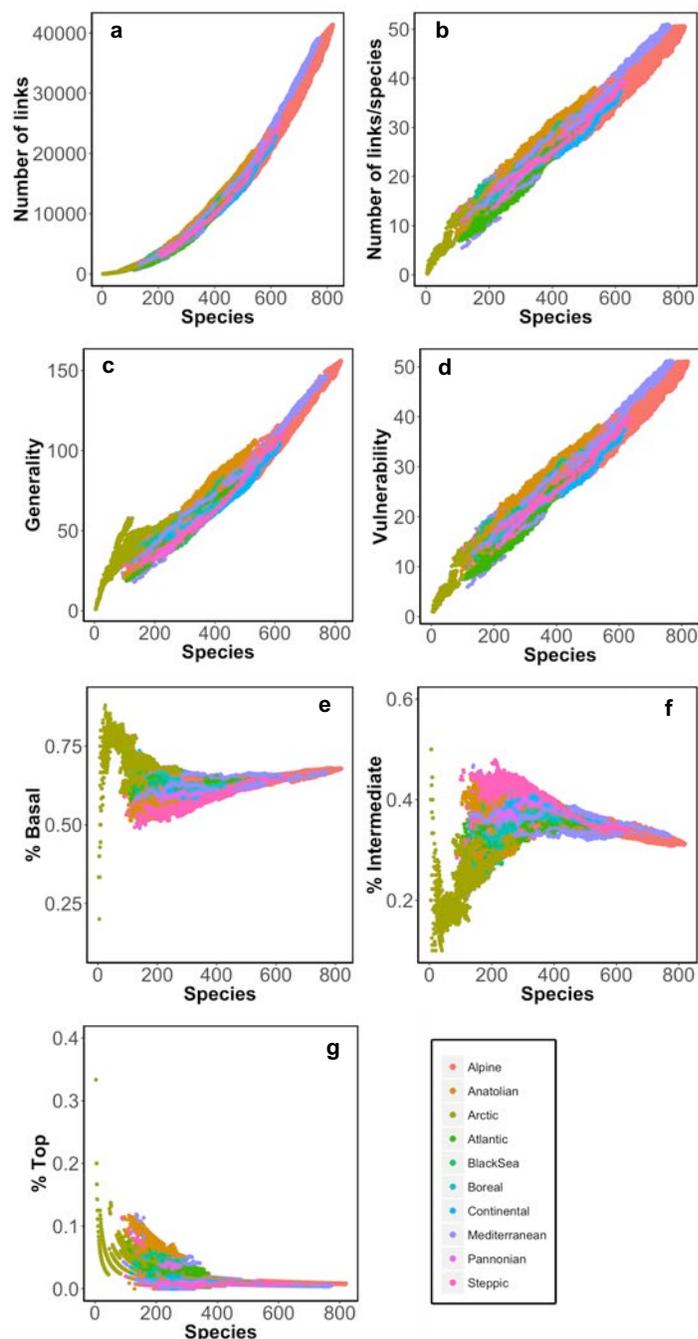


Figure 29. Relationship of network properties with species richness across biogeographical regions in Europe. (a) Number of links, (b) links per species, (c) mean generality, (d) mean vulnerability, (e) proportion of basal, (f) proportion of intermediate, (g) proportion of top species. For detailed description of network properties see methods. Notice that not all regions have the same species richness and, therefore, they are not represented along the whole range of species richness.

4.5 DISCUSSION

The spatial scaling of biodiversity has been traditionally understood as the scaling of species richness with area size [79], [81], [83]. However, species interactions are intrinsic components of ecological communities and as such, understanding how the network of interactions changes across spatial scales becomes fundamental to fully understand how biodiversity as a whole changes with area size [242]. We used the potential network of trophic interactions of the most European terrestrial vertebrates to analyse the spatial scaling of network structure at biogeographical scales. Although we found strong differences in the spatial scaling of network complexity across biogeographical regions, we also found striking universalities. The proportion of species per trophic level showed to be constant across spatial scales and biogeographical regions. Moreover, all the differences found in the spatial scaling of network complexity vanished once the geographical variation in species richness was accounted for.

The effect of species richness on many other aspects of network structure has been repeatedly studied in local communities [99], [100], [102], [254]. The variation in many food web properties is largely driven by changes in species richness [99], [102]. However, whether these correlations between species richness and network structure hold across large ranges of species richness and across different spatial scales was so far, unknown. Here we showed that species richness alone was enough to explain the geographical variability of the spatial scaling of network complexity. The number of links, links per species, mean generality and vulnerability showed extremely similar correlations (i.e., similar slopes of the linear regressions) with species richness across all biogeographical regions in Europe. This suggests that the patterns previously observed at local spatial scales also hold at large spatial scales, covering a much wider range of species richness (5-820); and across multiple biogeographical regions, where communities are subject to different environmental and historical conditions.

The scaling of the number of links with species richness is one of the most well-studied relationships in food web research [8], [104], [106]–[108], with two major hypotheses addressing it. While the ‘link-species scaling law’ [104] states that species interact with a constant number of species (roughly two) regardless of the total number of species in the network [104], [106], the ‘constant connectance hypothesis’ [107] states that it is the connectance (i.e., the fraction of potential interactions realized) of a community what is kept constant across food webs, irrespective of species richness. For this to happen, the number of links in a community needs to increase exponentially with species richness (slope 2 in log-log space). Empirically, the scaling of the number of links with species richness has been shown to fall in between the two hypotheses [8], [108]. Interestingly, we found a universal link-species relationship across biogeographical regions, indicating that at large spatial scales, although still falling in between both link

scaling hypotheses (slopes for all bioregions = 1.88 ± 0.14 ; Figure 29a; Appendix S4.3), the number of links increases exponentially with species richness.

The universalities found in the relationships between network complexity properties and species richness suggest that, in comparative network studies, controlling by the variation in the number of species might be enough to predict the changes in network complexity without necessarily accounting explicitly for the spatial scale considered in each study. However, species richness did not explain the patterns observed for the vertical diversity measures across spatial scales.

The distribution of species richness across trophic levels has long puzzled food web ecologists [106], [262], [263]. The fraction of species at different trophic levels was traditionally thought to be constant among networks across a wide range of species richness, and having a pyramidal shape where species richness consistently decreased with trophic level [106], [263]. However, further research found that although trophic diversity structure is generally pyramidal [264], the distribution of species richness per trophic level can also depend on external factors such as latitude, net primary productivity or ecosystem type [254], [264], and that it might depend on the total number of species in the community [101], [254], [264] and the spatial scale considered [101], [103]. In the case of our terrestrial vertebrate trophic webs, the relative proportions of species per trophic level were constant across biogeographical regions, spatial scales and species richness throughout Europe (Figure 28; Figure 29; Table 5). The proportions decreased from basal (0.62), to intermediate (0.35), to top species (0.03), generating a pyramidal shape in the food web. It is important to notice however that, because we are analysing the European terrestrial vertebrate community, basal species correspond to vertebrate species preying on basal resources (e.g., fish, invertebrates, plants, carrion), instead of corresponding to primary producers. Although what is basal markedly differs from the classical basal species concept in food webs, the conclusion holds for the universality of the proportions. What is less conclusive is the pyramidal structure of the diversity proportions per trophic level. The inclusion of lower trophic levels, e.g., including plants and invertebrates, might change the shape, but in any case, the proportion of basal species will always be larger than that of intermediate and top.

Given the influence of SARs in food web properties across spatial scales, focus should be placed on the understanding the possible factors and mechanisms promoting variability in SARs across locations and scales. Multiple mechanisms have been proposed to explain the shape of the species-area relationship (SAR) and, in particular, the scaling exponent (z) [94], [219]. Although at the European scale we recovered a multiphasic SAR with clear transitions between biogeographical regions (Appendix S4.6), elucidating the possible effect of different processes of speciation at different biogeographical regions

[81], [94], [219], we focused our analyses at the scale of the biogeographical regions, where the power function provided a good fit for all regions (Appendix S4.2; Appendix S4.5).

We observed quantitative differences in the shape of SARs across bioregions, indicating that these relationships might in fact vary across environmental or other ecological conditions. We identified the spatial variability of mean annual temperature and the spatial clustering of habitat types as the main determinants of the scaling exponent across Europe. The spatial variability in temperature characterizes one aspect of the environmental heterogeneity present in each biogeographical region, reflecting the increasing opportunity for a larger variety of species to be present as the heterogeneity increases- more niches available- and thus, promoting a faster accumulation of species with area. Niche differentiation theory predicts that the larger the range of environmental conditions, the larger the diversity due to niche differentiation and adaptability [265]–[268]. Similarly, habitat heterogeneity has been traditionally identified as an important underlying component of the scaling exponent of SAR [94], [250]–[252]. The larger the area sampled, the larger the number of different habitats encountered sustaining a larger set of species [250], [251]. Yet, the role of the spatial clustering of habitats on the scaling of biological diversity with area has been seldomly explored. Kolasa and colleagues [269], showed that the effects of habitat heterogeneity on the shape of SARs are scale dependent. That is, habitat heterogeneity at broader spatial scales produces higher z-exponents than at smaller spatial scale [269], suggesting that at small spatial scales a higher degree of habitat clustering produces faster accumulation of species with area. More directly, Altermatt and Holyoak [270], showed that the spatial aggregation of patch quality generally increases species beta-diversity, which underlies the slope of SARs. Similarly, it has been shown that species packaging at smallest scales leads to an initially steep increase of species with area [81], [94], [271].

While in our study these mechanisms affected the spatial scaling of network complexity only indirectly through the effect on the spatial scaling of species richness, environmental factors can directly affect network structure across spatial scales. Habitat structure has been shown to have direct effects on biotic interactions. For example, it has been shown that habitat loss or modification can alter biotic interactions [205], [206], [209] and the functions species perform [207], [272], without large variations in species richness, highlighting the need of incorporating information on the spatial scaling of network structure to fully assess the impacts of habitat modification on biodiversity and ecosystem functioning [207], [208]. Moreover, landscape heterogeneity can promote the emergence of species sorting (i.e., different habitat preferences between species), which can generate compartments in the network and promote a modular or compartmented structure [200], [201]. Even more concretely, recent research has

shown the effect of spatial filters and climate on the modularity of the plant-hummingbird metaweb from six different Brazilian biomes, which resulted in six modules conforming with the vegetation domains [273]. Our food webs, however, presented extremely low values of modularity. This is most likely due to the potential nature of the biotic interactions considered in our study. A network is considered modular when interactions between species are more numerous or stronger within a given compartment than between compartments [200], [201]. Including all potential interactions between species might prevent modularity to emerge. However, the results obtained are consistent with the previous findings for modelled food webs in homogeneous environments (chapter 2), and empirical NARs (chapter 3): modularity is scale-invariant, whether the exact value is high or low, it is constant across spatial scales.

Similarly, the potential nature of the metaweb biases the proportion of species per trophic level towards intermediate species in detriment of top species, because it is very unlikely for a given species not to have any potential predator. However, all biogeographical regions should be equally affected by this possible bias, which ensures the prevalence of the universalities found across biogeographical regions.

Conclusions: We showed that a geographical variation in the spatial scaling of network structure across Europe exists, but that it is mostly determined by the variation in the shape of SARs across biogeographical regions in Europe. Important universalities emerged regarding the relationship of network properties with species richness and the proportion of species per trophic level, which were constant across spatial scales and biogeographical regions. The use of the potential network of trophic interactions of the European terrestrial community at the continental scale, allowed us to analyse the geographical variation of the effect of area on network properties, which can open new avenues to explore the effect of different environmental factors on the spatial scaling of network structure. NARs can provide new insights to analyse and understand ecological communities and how they are affected by different processes at each spatial scale.

Author contributions:

NG, JMM and WT designed research. NG and ML conducted research and analysed the data with feedback from all the co-authors. NG wrote the manuscript with feedback from all the co-authors. LM, FF, WT contributed the data.

SUPPLEMENTARY MATERIAL CHAPTER 4

Content

- **Appendix S4.1.** Statistical analyses for the determinants of the Species-Area relationship.
- **Appendix S4.2.** Power function fit for all network properties analysed.
- **Appendix S4.3.** Relationships of network properties with species richness.
- **Appendix S4.4.** Different increase in species richness across trophic levels.
- **Appendix S4.5.** Species-Area relationship across biogeographical regions in Europe.
- **Appendix S4.6.** Contribution of each biogeographical region to the global species-area relationship in Europe.

Appendix S4.1. Statistical analyses for the determinants of the Species-Area relationships.

Variation across NARs scaling in different European bioregions was hypothesised to be explained by a set of environmental and habitat complexity variables (see methods). However, the high correlation detected among many of the variables (Fig. S5.1) suggested a potentially strong multi-collinearity effect on the explanatory power of these variables. Predictor variables considered included: The total area of the bioregion (Total Area), the Bray-Curtis dissimilarity between habitat composition across cells of the gridded map of the bioregion (Bray-Curtis), Moran's I spatial autocorrelation index across habitats within each bioregion, number of habitats (No. of habitats), average of the mean annual temperature across cells in the bioregion (Mean Temp.), variability (measured as the standard deviation) in the average of the mean annual temperature across cells in the bioregion (SD Mean Temp.), temperature seasonality during the year averaged across map cells (Mean Seas.), and variability (i.e., SD) of temperature seasonality across cells (SD Seas.).

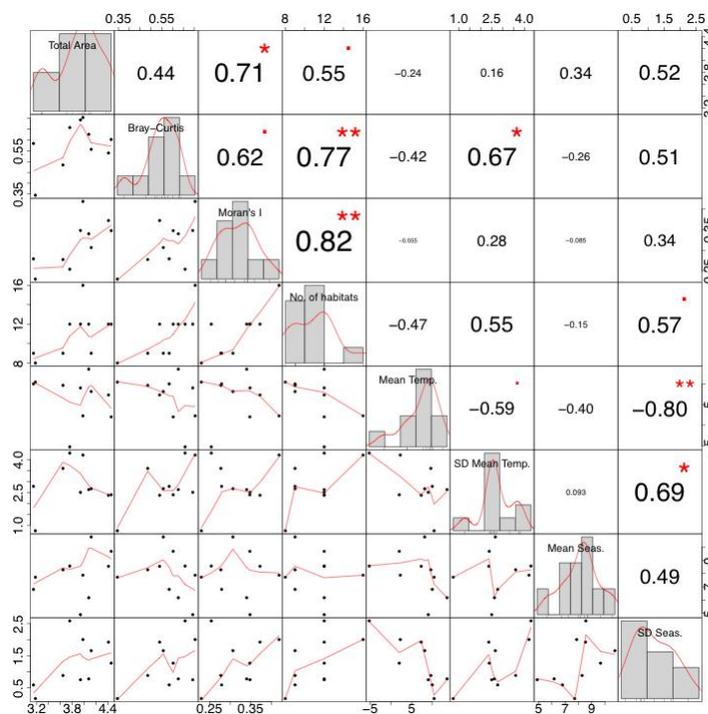


Figure S3.5. Correlation among predictor variables for the scaling of NARs. Scatterplots of the pairwise relationships between variables and their distributions are shown. Numbers on the upper triangle of the matrix are Pearson's correlation coefficients and stars indicate their significance based on the p-value (< 0.05 , * < 0.01 , ** < 0.001). Names of the variables are explained in the text.

Because of the potential effects of multi-collinearity, we used Commonality Analysis (CA) [261] to find the best predictors for the scaling exponent (z) of NARs. In brief, CA is a statistical technique that offers information of the statistical relationship between predictor variables when they are used to explain a dependent variable using linear regression. By considering correlations among predictors, CA calculates variance inflation factors (VIF). Additionally, CA provides information on the fraction of the model fit that is due to suppression among predictor variables, their unique vs. common contributions to the model explanatory abilities, and the mismatch between the variables' coefficient when used alone vs. when considered jointly in the linear regression. All this information can be used to select the variables that explain best the model fit, by removing those that artificially inflate the model's fit. Here we provide an example of how CA was used to remove variables having a potential artificial effect on the model's capacity to explain variability in the data. Total Area was removed from the analysis beforehand due to its low explanatory power detected through previous hierarchical partitioning analysis. Inputting the remaining set of variables to the CA results in the values shown in Table S3.5.

Table S3.5. Results of CA performed over the whole set of variables. This table shows the regression coefficients both jointly and in isolation, the standard error of the mean, confidence intervals, p-values of significance based on 200 bootstrapping iterations, total contribution of the variable to the model (split in unique and common) and the variance inflation factor (VIF) for all predictor variables considered in the model.

Variable	rs	betas	StdErr	Clinf	Clsup	p-value	Unique	Common	Total	VIF
Bray-Curtis	0.723	0.112	0.191	-0.152	0.349	0.616	0.003	0.513	0.515	5.097
Morans I	0.515	-0.539	0.317	-0.551	0.000	0.231	0.021	0.240	0.261	13.972
No. of Habitats	0.692	0.832	0.360	0.000	0.842	0.147	0.038	0.433	0.472	18.096
Mean Temp.	-0.340	0.922	0.248	0.000	1.266	0.065	0.099	0.015	0.114	8.580
SD Mean Temp.	0.888	0.672	0.151	0.000	0.797	0.047	0.143	0.635	0.777	3.169
Mean Seas.	-0.058	0.113	0.191	-0.089	0.307	0.613	0.003	0.001	0.003	5.072
SD Seas.	0.655	0.514	0.206	0.000	0.874	0.130	0.045	0.378	0.423	5.916

Model fit resulting from the CA considering the whole set of predictor variables is high (98.56% of the variance explained). However, the VIFs (Table S5.1) and the percentage of suppression in the model fit (176.79%) detected were both high. This suggests that at least some of the variables have an artificial (i.e., indirect) effect on model fit, and hence its explanatory capabilities. From the values shown in Table S3.5, we can see that the total contribution to model fit of mean temperature seasonality is almost none (0.0033), so this is a good candidate to remove from the analysis. Also, the VIF for the number of habitats is extremely high (18.096), making this variable also a good candidate to be removed.

We removed predictor variable from our set following the type of criteria outlined above until the suppression of model fit due to multi-collinearity was reduced to 0% and we ended up with two main predictors that are able to explain 85.53% of the model variability: the mean annual temperature variability across the bioregion (SD Mean Temp.) and the Moran's I index of habitats spatial autocorrelation (Moran's I). Linear regression of this two predictors on NARs scaling exponent show that there is a significant relationship between predictors and dependent variables ($R^2 = 0.8553$, p -values = 0.00105 and 0.09328 respectively).

Thus, we can conclude that annual temperature variability and habitat clustering (i.e., spatial autocorrelation) within bioregions are faithful predictors of the scaling velocity of species number with area. Places with more variability in temperature and higher habitat clustering tend to accumulate species faster as area sampled increases.

Appendix S4.2. Power function fit for all network properties analysed. Fit of each network property of each biogeographical region to a power function ($f(x) = cx^z$), where c is the scaling factor and z is the exponent parameter that determines the function's rates of growth and its overall shape. We used nonlinear least squares (NLS) with the 'nls' function in R.

Parameters	Region	Property	Estimate	Std. Error	t value
c	Alpine	species	24.08	0.07	368.28
z	Alpine	species	0.38	0.00	1215.59
c	Alpine	links	36.28	0.21	169.19
z	Alpine	links	0.77	0.00	1137.03
c	Alpine	links per sp	2.48	0.01	380.35
z	Alpine	links per sp	0.32	0.00	1054.93
c	Alpine	generality	4.01	0.01	321.15
z	Alpine	generality	0.39	0.00	1088.58
c	Alpine	vulnerability	2.56	0.01	381.82
z	Alpine	vulnerability	0.32	0.00	1051.85
c	Anatolian	species	64.82	0.08	805.00
z	Anatolian	species	0.25	0.00	1572.03
c	Anatolian	links	355.86	0.89	400.39
z	Anatolian	links	0.48	0.00	1526.19
c	Anatolian	links per sp	6.25	0.01	953.13
z	Anatolian	links per sp	0.21	0.00	1574.16
c	Anatolian	generality	11.84	0.02	603.67
z	Anatolian	generality	0.26	0.00	1216.00
c	Anatolian	vulnerability	6.81	0.01	938.04
z	Anatolian	vulnerability	0.20	0.00	1477.01
c	Arctic	species	19.79	0.06	353.62
z	Arctic	species	0.31	0.00	876.44
c	Arctic	links	109.25	0.47	230.24
z	Arctic	links	0.46	0.00	854.74
c	Arctic	links per sp	3.56	0.01	376.94
z	Arctic	links per sp	0.20	0.00	604.50
c	Arctic	generality	14.61	0.02	612.75
z	Arctic	generality	0.16	0.00	789.82
c	Arctic	vulnerability	4.03	0.01	382.12
z	Arctic	vulnerability	0.19	0.00	572.92
c	Atlantic	species	64.51	0.09	687.11
z	Atlantic	species	0.22	0.00	1259.51

c	Atlantic	links	154.14	0.61	253.75
z	Atlantic	links	0.50	0.00	1082.36
c	Atlantic	links per sp	4.14	0.01	531.01
z	Atlantic	links per sp	0.21	0.00	950.50
c	Atlantic	generality	11.34	0.02	545.72
z	Atlantic	generality	0.21	0.00	975.75
c	Atlantic	vulnerability	4.34	0.01	539.62
z	Atlantic	vulnerability	0.21	0.00	945.91
c	BlackSea	species	95.56	0.35	276.80
z	BlackSea	species	0.22	0.00	392.89
c	BlackSea	links	602.10	4.20	143.34
z	BlackSea	links	0.44	0.00	425.05
c	BlackSea	links per sp	8.12	0.02	416.42
z	BlackSea	links per sp	0.19	0.00	506.50
c	BlackSea	generality	20.45	0.05	402.14
z	BlackSea	generality	0.19	0.00	506.77
c	BlackSea	vulnerability	8.62	0.02	427.01
z	BlackSea	vulnerability	0.18	0.00	502.09
c	Boreal	species	89.41	0.03	2636.06
z	Boreal	species	0.15	0.00	3765.94
c	Boreal	links	845.54	0.48	1759.65
z	Boreal	links	0.25	0.00	4166.94
c	Boreal	links per sp	9.91	0.00	4607.56
z	Boreal	links per sp	0.09	0.00	3975.52
c	Boreal	generality	27.15	0.01	4069.75
z	Boreal	generality	0.09	0.00	3408.63
c	Boreal	vulnerability	10.09	0.00	4600.91
z	Boreal	vulnerability	0.09	0.00	3947.83
c	Continental	species	54.70	0.05	1088.57
z	Continental	species	0.24	0.00	2444.40
c	Continental	links	147.24	0.34	434.07
z	Continental	links	0.50	0.00	2076.06
c	Continental	links per sp	4.79	0.00	961.13
z	Continental	links per sp	0.20	0.00	1797.57
c	Continental	generality	8.18	0.01	777.01
z	Continental	generality	0.25	0.00	1818.62
c	Continental	vulnerability	4.92	0.01	969.81

z	Continental	vulnerability	0.20	0.00	1793.80
c	Mediterranean	species	50.34	0.10	527.94
z	Mediterranean	species	0.29	0.00	1331.51
c	Mediterranean	links	92.96	0.47	196.96
z	Mediterranean	links	0.64	0.00	1132.57
c	Mediterranean	links per sp	3.26	0.01	458.52
z	Mediterranean	links per sp	0.29	0.00	1161.26
c	Mediterranean	generality	6.15	0.01	430.41
z	Mediterranean	generality	0.33	0.00	1267.16
c	Mediterranean	vulnerability	3.37	0.01	470.24
z	Mediterranean	vulnerability	0.29	0.00	1179.52
c	Pannonian	species	202.54	0.11	1900.83
z	Pannonian	species	0.08	0.00	946.36
c	Pannonian	links	2599.35	3.38	768.50
z	Pannonian	links	0.16	0.00	811.17
c	Pannonian	links per sp	13.02	0.01	1342.74
z	Pannonian	links per sp	0.08	0.00	709.28
c	Pannonian	generality	32.94	0.02	1595.18
z	Pannonian	generality	0.08	0.00	815.36
c	Pannonian	vulnerability	13.40	0.01	1399.61
z	Pannonian	vulnerability	0.08	0.00	713.57
c	Steppic	species	58.42	0.09	660.96
z	Steppic	species	0.24	0.00	1406.98
c	Steppic	links	127.96	0.52	246.04
z	Steppic	links	0.54	0.00	1196.74
c	Steppic	links per sp	4.54	0.01	604.21
z	Steppic	links per sp	0.22	0.00	1147.99
c	Steppic	generality	6.70	0.01	458.81
z	Steppic	generality	0.28	0.00	1158.95
c	Steppic	vulnerability	4.63	0.01	591.44
z	Steppic	vulnerability	0.21	0.00	1119.19

Appendix S4.3. Relationships of network properties with species richness.

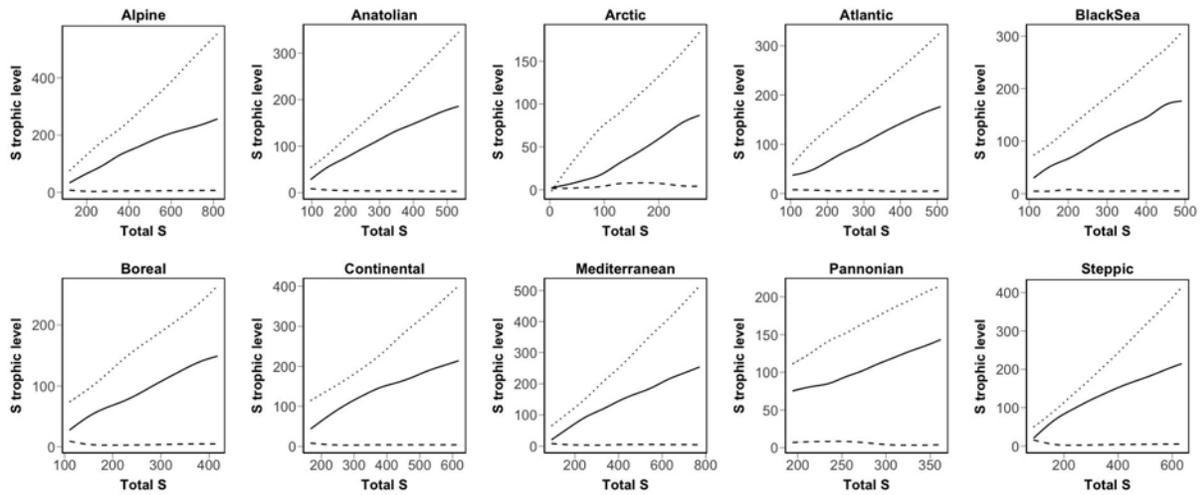
Linear model results for the correlations of all network properties with species richness at each biogeographical region. Estimates, T values and adjusted-R² are provided for each correlation.

	Region	Property	Estimate	Std. Error	t value	Adjusted-R ²
log10(species)	Alpine	log10(links)	1.85	0.00	10072.70	0.99
log10(species)	Anatolian	log10(links)	1.84	0.00	8154.93	1.00
log10(species)	Arctic	log10(links)	1.75	0.00	5231.67	0.99
log10(species)	Atlantic	log10(links)	2.05	0.00	6711.62	0.99
log10(species)	BlackSea	log10(links)	1.79	0.00	2597.88	0.99
log10(species)	Boreal	log10(links)	1.60	0.00	16356.72	0.99
log10(species)	Continental	log10(links)	1.88	0.00	14389.49	0.99
log10(species)	Mediterranean	log10(links)	2.00	0.00	12027.21	1.00
log10(species)	Pannonian	log10(links)	2.08	0.00	2708.74	0.99
log10(species)	Steppic	log10(links)	1.91	0.00	11793.12	0.99
species	Alpine	links per sp	0.06	0.00	4635.26	0.97
species	Anatolian	links per sp	0.06	0.00	4086.80	0.98
species	Arctic	links per sp	0.06	0.00	1973.02	0.92
species	Atlantic	links per sp	0.06	0.00	3854.87	0.97
species	BlackSea	links per sp	0.06	0.00	1101.74	0.94
species	Boreal	links per sp	0.04	0.00	6228.28	0.96
species	Continental	links per sp	0.06	0.00	6705.26	0.97
species	Mediterranean	links per sp	0.07	0.00	7570.58	0.99
species	Pannonian	links per sp	0.07	0.00	1454.16	0.96
species	Steppic	links per sp	0.06	0.00	6265.62	0.98
species	Alpine	generality	0.18	0.00	4522.76	0.97
species	Anatolian	generality	0.20	0.00	3204.82	0.98
species	Arctic	generality	0.14	0.00	1853.78	0.91
species	Atlantic	generality	0.17	0.00	4176.65	0.97
species	BlackSea	generality	0.15	0.00	964.44	0.92
species	Boreal	generality	0.10	0.00	3137.42	0.85
species	Continental	generality	0.18	0.00	7902.40	0.98
species	Mediterranean	generality	0.21	0.00	9663.55	0.99
species	Pannonian	generality	0.17	0.00	1289.39	0.95
species	Steppic	generality	0.20	0.00	6106.53	0.98
species	Alpine	vulnerability	0.06	0.00	4690.57	0.97
species	Anatolian	vulnerability	0.06	0.00	3738.19	0.98
species	Arctic	vulnerability	0.06	0.00	1738.77	0.90
species	Atlantic	vulnerability	0.06	0.00	3809.60	0.97
species	BlackSea	vulnerability	0.06	0.00	976.57	0.92

species	Boreal	vulnerability	0.04	0.00	6159.13	0.96
species	Continental	vulnerability	0.06	0.00	6655.23	0.97
species	Mediterranean	vulnerability	0.07	0.00	7830.15	0.99
species	Pannonian	vulnerability	0.07	0.00	1450.81	0.96
species	Steppic	vulnerability	0.06	0.00	5708.38	0.98
species	Alpine	top	-9E-06	1E-08	-623.49	0.41
species	Anatolian	top	-5E-05	1E-07	-377.46	0.35
species	Arctic	top	-2E-04	3E-07	-590.92	0.51
species	Atlantic	top	-6E-05	1E-07	-582.11	0.40
species	BlackSea	top	-6E-05	3E-07	-217.94	0.36
species	Boreal	top	-7E-06	2E-08	-369.39	0.07
species	Continental	top	-2E-05	8E-09	-2064.19	0.74
species	Mediterranean	top	-1E-05	2E-08	-624.26	0.35
species	Pannonian	top	-1E-04	7E-07	-218.22	0.35
species	Steppic	top	-2E-06	2E-08	-105.93	0.01
species	Alpine	intermediate	-7E-05	1E-07	-630.77	0.41
species	Anatolian	intermediate	-1E-04	3E-07	-371.57	0.34
species	Arctic	intermediate	6E-04	6E-07	1057.88	0.77
species	Atlantic	intermediate	6E-05	2E-07	332.27	0.18
species	BlackSea	intermediate	7E-05	5E-07	138.04	0.19
species	Boreal	intermediate	7E-05	2E-07	369.31	0.07
species	Continental	intermediate	-1E-04	7E-08	-2108.13	0.74
species	Mediterranean	intermediate	-8E-05	1E-07	-778.00	0.46
species	Pannonian	intermediate	2E-04	1E-06	209.80	0.33
species	Steppic	intermediate	-2E-04	1E-07	-2021.85	0.84
species	Alpine	basal	8E-05	1E-07	714.93	0.47
species	Anatolian	basal	2E-04	3E-07	620.16	0.59
species	Arctic	basal	-4E-04	7E-07	-635.08	0.54
species	Atlantic	basal	3E-06	2E-07	20.12	0.00
species	BlackSea	basal	2E-05	4E-07	39.47	0.02
species	Boreal	basal	-6E-05	2E-07	-304.86	0.05
species	Continental	basal	2E-04	7E-08	2348.63	0.78
species	Mediterranean	basal	1E-04	9E-08	1136.23	0.64
species	Pannonian	basal	-7E-05	9E-07	-73.29	0.06
species	Steppic	basal	2E-04	1E-07	1917.09	0.82

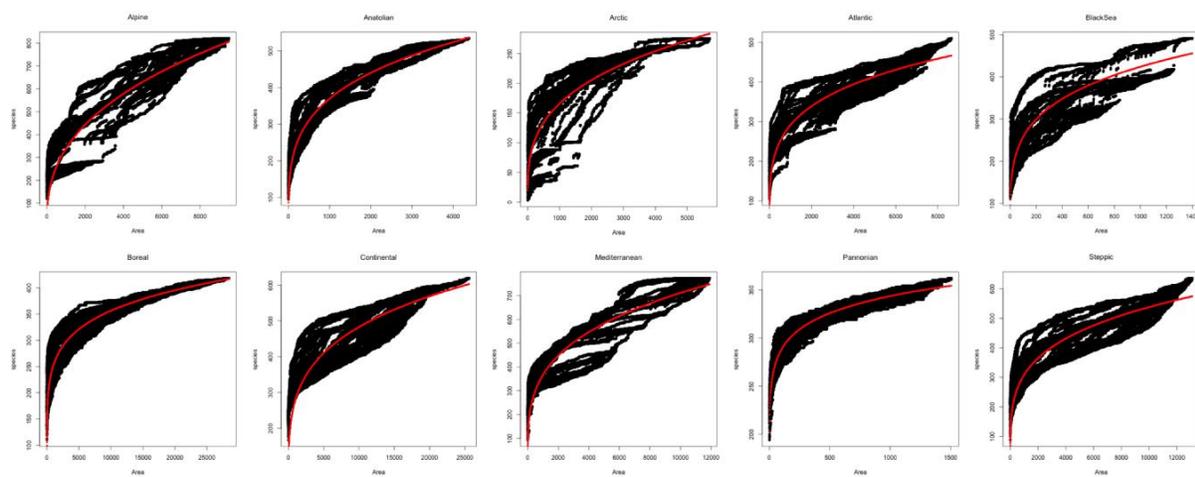
Appendix S4.4. Different increase in species richness across trophic levels.

Relationship between the number of species in each trophic level with the total number of species in each biogeographical region in Europe. Dotted line, basal species; black line, intermediate species; dashed line, top species. Shaded areas correspond to 95% confidence intervals.

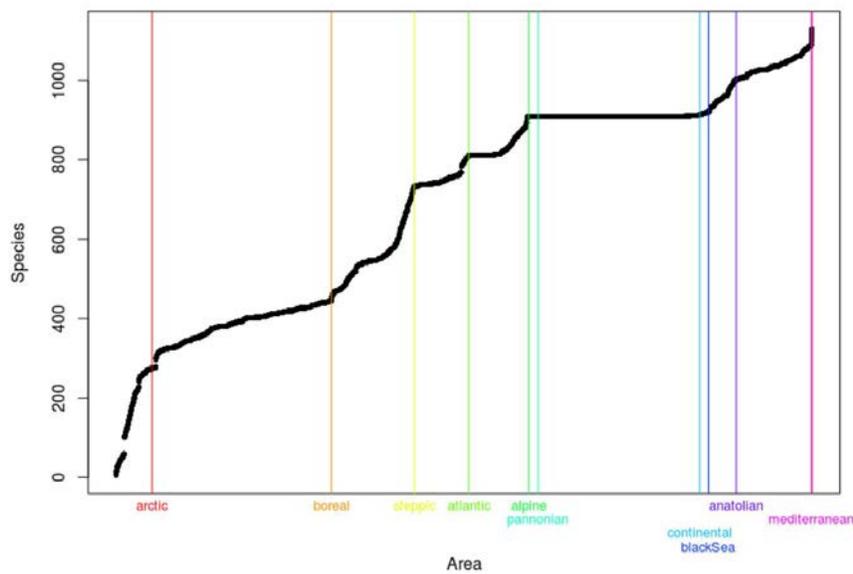


Appendix S4.5. Species-Area relationship across biogeographical regions in Europe.

Relationship between the number of species with area in each biogeographical region in Europe. Black dots correspond to data points and red line correspond to the predicted values from the power function fit.



Appendix S4.6. Contribution of each biogeographical region to the global species-area relationship in Europe. Relationship between the number of species with area across all the European range considering the contribution of each biogeographical region. Notice that for the realization of this figure we used a linear neighbouring aggregation following the north-south gradient instead of the method used in the rest of the paper. Each colored line represent the end of all the cells corresponding to a given biogeographical region. Therefore, the increase in the number of species from one region to the next correspond to the sampling of new species not found in the previous region. The pattern observed here changes when following the opposite latitudinal gradient. That is, starting with the species rich regions, such as Mediterranean.



GENERAL DISCUSSION AND CONCLUSIONS

Ecological network research and biogeography have been traditionally developed in isolation. Although challenging, the integration is both possible and necessary if we aim to better understand ecological communities and how they are likely to respond to perturbations in an increasingly human-modified world. The main objective of this thesis has been to benefit from the integration of the two fields to understand how ecological communities are structured in space and how they are influenced by large-scale processes, such as climate or habitat heterogeneity. In this general conclusion, I firstly summarize the main and novel contributions of the chapters, I then discuss the limitations of the approach and I finally propose a number of future perspectives to advance towards a deeper understanding of macroecological networks.

MAIN CONTRIBUTIONS

Is there a geographical gradient in the structure of ecological networks?

The latitudinal variation in biotic specialization has long interested ecologists. Although biotic specialization has historically been thought to be higher in more constant environments [63], [65], [71], [119], recent studies have challenged this view. While some authors showed an increase in network specialization towards the tropics [70]–[72], [78], others found the opposite [64], or no latitudinal trend at all [75], [76]. However, all studies have focused on specialization across local communities, ignoring how specialization at larger spatial extents varies along the same biogeographical gradient.

In the first chapter of the thesis, I addressed the geographical variation in network structure by analysing biotic specialization from different perspectives (i.e., not only from the consumers' perspective but also from the resources one and at the network level) and at different spatial scales (i.e., local and regional). I showed that the geographical variation in biotic specialization is not universal. It depends on both the facet of biotic specialization analysed and the spatial scale of observation. Indeed, local and regional networks displayed very different patterns along the gradients of climatic constancy. While at the regional scale, biotic specialization did not show a latitudinal gradient, at the local scale networks in more constant environments were less connected, consumers overlapped their niches less, and preys were attacked by fewer predators. In contrast, consumers were more generalists in more constant environments, contrary to the hypothesized

latitudinal gradient on niche breadth [34], [63], [119]. The opposite geographical patterns in biotic specialization between consumers and resources perspectives, highlighted the importance of analysing different aspects of network structure to fully understand the geographical patterns in biotic specialization, as recently shown by Dalsgaard and colleagues [74]. Interestingly, I found a decrease of the consumer:resource ratio with environmental constancy at local scales while at the regional scale, it did not change along the gradient. Therefore, in more constant environments, local networks had a smaller proportion of consumers per resources than regional networks, and in more fluctuating environments, local networks had a larger proportion of consumers per resources than regional networks.

Then the question was, how could the same “potential” regional network lead to opposite “realized” local networks along the climatic constancy gradient? I suggested β -diversity as a possible explanation. Specifically, the differences in β -diversity between local consumer and resource assemblages along the gradients of climatic constancy. In the tropics (i.e., less fluctuating regions), if the spatial turnover of consumers is larger than that of resources, the number of consumers increases faster than the number of resources when local networks are aggregated into regional webs. In contrast, in more fluctuating areas larger spatial turnover of resources should result in a faster increase in the number of resources when scaling up in space.

These results therefore unveiled, for the first time, not only the importance of considering the spatial scale of observation to better understand the patterns of network structure along geographical gradients, but also the potential power of understanding the spatial scaling of network structure to elucidate the role of different spatial processes in a given region.

How does network structure change with area size?

The second, third and fourth chapters of the thesis were fully devoted to understand and analyse the spatial scaling of network structure. I firstly identified and theoretically explored the main mechanisms underlying the changes in network structure with area size. Then, I compiled a large set of ecological networks from different ecosystems and biomes across the globe to empirically test the theoretical predictions.

The theoretical framework revealed a number of Network-Area Relationships (NARs) for multi-trophic communities emerging from different spatial processes, such as, the differences in the Species-Area relationship (SARs) across trophic levels, the preferential selection of generalist species in small islands, and the effect of beta-diversity caused by dispersal limitation. Network complexity

increased with area size together with the proportion of specialised species, which also increased with area, showing that they were only able to colonize and persist when the island was large enough. Network vertical diversity also increased with area size via the increase in the proportion of species at intermediate positions of the food web, which had omnivorous links and caused the increase of the length of the food chains. In contrast, network modularity remained constant across spatial scales.

The large set of ecological networks comprising different types of interactions and sampling methodologies, allowed me to test these theoretical predictions. I found that ecological communities become more complex as area size increases, showing an increase in the number of links, in the number of links per species and in the mean number of resources a consumer has. Interestingly, as predicted theoretically, I found an increase in the proportion of specialist species with area, confirming that specialist species require larger areas to be found and, therefore, might be more vulnerable to reductions of available habitats.

In contrast, the proportion of consumers and resources present in a community (measured as the consumer:resource ratio) did not show a clear trend with area across all data sets. However, in chapter 4, where I deepen in the analyses of the spatial scaling of network structure across biogeographical regions in Europe, I found the proportions of species per trophic level to be remarkably constant across spatial scales and across biogeographical regions, which suggested that multi-trophic communities preserved basic structural properties across spatial scales. If we look here at the proportion of species per trophic level in the rest of the multi-trophic communities used in chapter 3, we see that, although differing largely among data sets, most food webs do show constant proportions of species per trophic level across spatial scales, also reflected by the low z-exponents of the Ratio-Area relationship (Figure 30; Appendix S4.2.). Therefore, while mutualist and antagonist bipartite networks did not show consistent patterns in the proportion of species per trophic level when increasing area size, food webs seem to preserve the proportions across spatial scales.

Finally, network modularity did not show strong changes with area size across the empirical communities. Yet, for those communities that did show a change in network modularity it followed a decreasing trend with area. However, neither in the theoretical models nor in the ecological communities analysed, habitat heterogeneity was considered and analysed explicitly. A

fundamental aspect was, therefore, to understand whether there are universal patterns for the scaling of network structure with area size and which are the possible sources of variation.

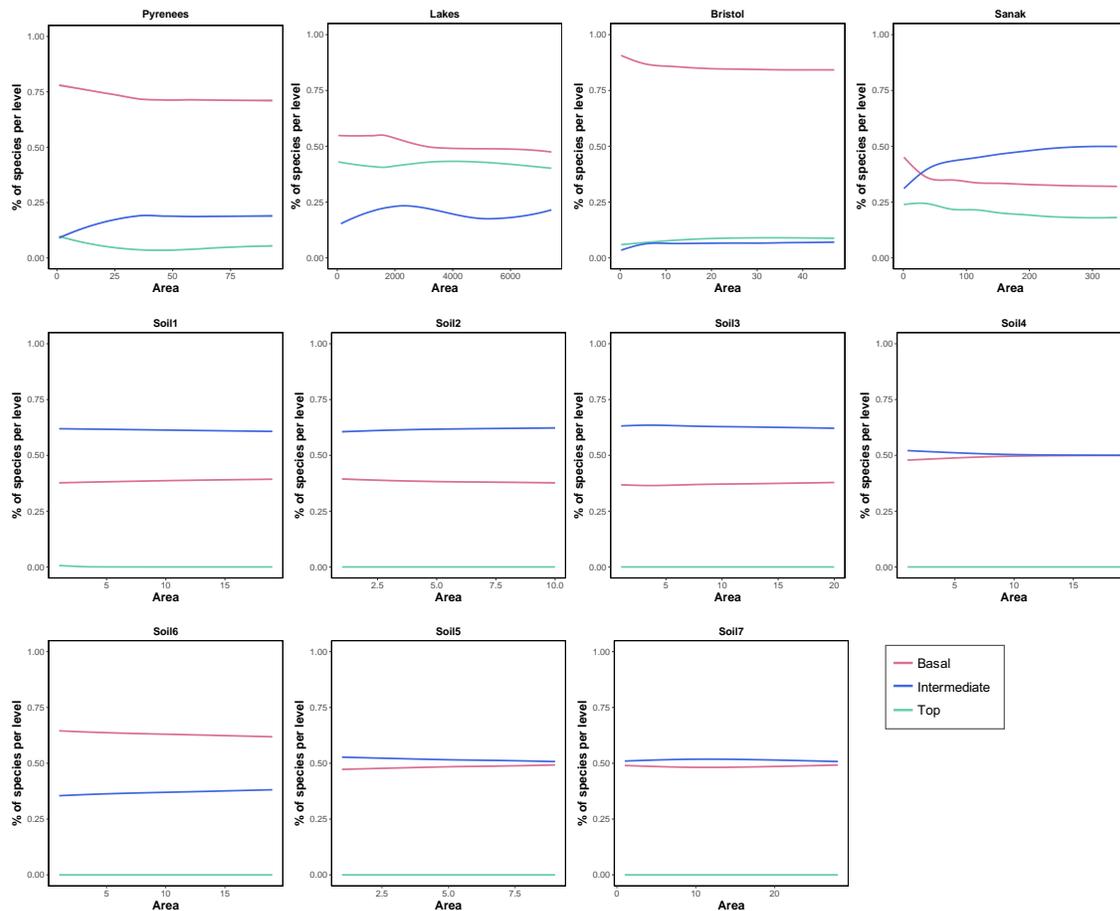


Figure 30. Relationship of the percentage of basal, intermediate and top species with area for all data sets of multi-trophic communities used in chapter 3. For a detailed description of the datasets and the methodology used to calculate the proportion of species per trophic level, see chapter 3. Notice that the proportion of top species in datasets Soil 1-7 are extremely close to zero due to the difficulty of finding in soil food webs species that are not being consumed by any other species.

Are the changes in network structure with area size universal?

I analysed whether there exist generalities in the changes of network structure across spatial scales in chapter 3 and 4. The use of multiple types of data in chapter 3 allowed me to determine whether the observed network-area relationships (NARs) were universal and how their specific shape was affected by the underlying ecological processes captured by each data type. All properties related to network complexity increased with area size following a power law for all data categories. Yet, they showed differences in most of the scaling exponents. Islands showed the slowest increase of network complexity with area, especially for the spatial scaling of the number of links per species, which indicates that in islands species gain less links as area size increases, suggesting that the turnover of links (i.e., Links β -diversity) independent of the turnover of species composition might be smaller in islands.

Similarly, in chapter 4, I observed differences in the scaling exponents of NARs across biogeographical regions. However, as previously suggested in the theoretical framework, I found that most of the differences disappeared when the differences in the spatial scaling of species richness were accounted for. Instead, network vertical diversity properties, such as the proportions of species per trophic level, remained remarkably constant along the gradient of species richness. The effect of species richness on network structure has been repeatedly studied in local communities [99], [100], [102], [254]. The variation in many food web properties is largely driven by changes in species richness [99], [102]. However, in chapter 4 I showed how these correlations hold across large ranges of species richness and across different spatial scales and biogeographical regions, where communities are subject to different environmental and historical conditions. I showed that species richness alone is enough to explain the geographical variability of the spatial scaling of network complexity in Europe. But further research is needed to disentangle the universality of the effects of species richness on the spatial scaling of all network properties across different ecological systems.

PERSPECTIVES

Species geographical ranges and ecological networks

Species geographical ranges are at the base of biogeographical research. They constitute one of the fundamental ecological and evolutionary characteristics of species and they are considered strong predictors of species extinction risks [274]. The influence of biotic interactions on

determining species geographical ranges has long been questioned [31], [51], [275]. They have been recently shown to not only limit species current geographical ranges but also to influence species responses to climate change and therefore, the limits of their future distribution [36], [276], [277]. Inversely, although more empirical evidence is needed, species geographical range size has correlated positively with species diet breadth [31], [166], [167], [278]. However, much less is known about how the combination of species distributions determine the structure of local ecological communities or the spatial scaling of network structure in a given region. In chapter 1, I indirectly link species geographical ranges to the structure of ecological communities and their spatial scaling by considering species beta-diversity as the underlying mechanism promoting the changes in network structure across spatial scales. Species turnover in a given region is largely determined by their geographical range limits. If geographical range sizes differ across trophic levels, beta-diversity patterns will also be different and, therefore, we will observe changes in network structure across spatial scales (Figure 31). In particular, our empirical evidence in chapter 1 suggests that consumers will tend to have smaller ranges than resources in regions with more environmental constancy, such as the Tropics, while in more fluctuating areas, consumers and resources will tend to have similar ranges.

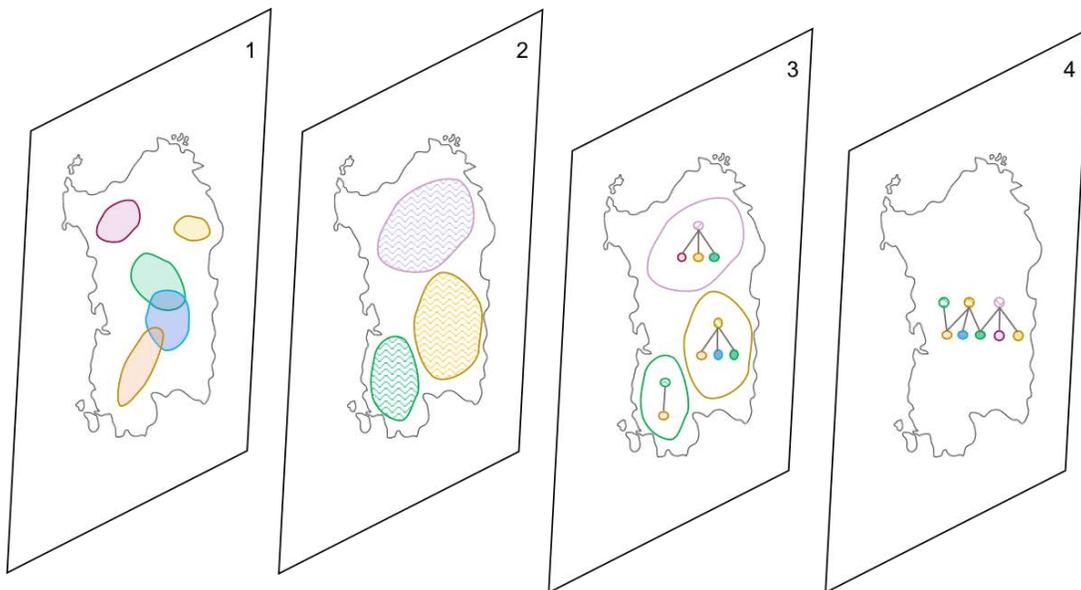


Figure 31. Combination of species geographical ranges, beta-diversity and biotic interactions. The first and second layers represent resources and consumers geographical ranges, respectively. The third layer shows local interactions between consumers and resources depending on their geographical ranges overlap. The fourth layer represents the regional network resulting from the aggregation of all biotic interactions.

In the cartoon representation depicted in figure 31, resources geographical ranges are smaller than consumers geographical ranges, which results in a larger proportion of resources per consumer that allows them to not specialize in a unique resource. On the contrary, if consumers geographical ranges would be smaller than that of resources, the patterns of biotic specialization would change showing a higher degree of biotic specialization. Or if both consumers and resources ranges would be equally smaller, we could predict patterns of reciprocal specialization emerging from the ranges overlap.

In chapter 4, I directly used species ranges to filter species interactions by constraining them to only those species whose ranges overlapped in space. However, I did not establish direct links between the distribution of the geographical ranges of the species present in a community of a given region with the patterns observed of local network structure and its spatial scaling. Establishing these direct relationships would allow us to predict a number of structural properties of the network for a region of interest, such as patterns of biotic specialization. This is not only interesting on itself, but it will also inform on the effects of perturbations, like habitat loss, on the structure of ecological communities only from the species geographical ranges and basic information on their biotic interactions. This new avenue for the integration of biogeography and ecological networks would potentially represent a step forward for the understanding and use of macroecological networks in conservation.

Spatial scaling of quantitative networks and ecosystem functioning

In all chapters of the thesis I have used binary networks. That is, I focused on the topological properties of the networks instead of using quantified information on the interaction strength between species. As previously explained in chapter 1, data on the structure and strength of ecological interactions at large spatial scales is still not available. Most data on ecological networks are snapshots in time and space [140]. However, both species interactions and their strengths vary over time and space depending on factors such as, abiotic conditions, population densities, predator switching or due to non-linear functional responses [24], [141]–[144]. Therefore, averaging interaction strengths across local communities to estimate the spatial scaling of interaction strengths seems both problematic and unrealistic. Direct measures of interaction strengths accounting for these variations in population densities and functional responses across spatial scales are needed to progress towards the spatial scaling of quantitative networks.

Interaction strengths in ecological networks have been proven key to understand different aspects of community dynamics and stability [212], [213], [216], [279], and have been related to the effects of different perturbations on ecosystem functioning [45], [47], [272], [280], [281]. Understanding how quantitative networks change across spatial scales would, therefore, open new possibilities to explore how community stability and functioning change with area size and how are they affected by the different processes that are at play at each spatial scale. However, this first requires an important methodological work on how to scale interaction strength with space.

Determinants of the shape of NARs

Throughout the thesis, I explored the spatial scaling of network structure by determining the mechanisms behind changes in community structure across spatial scales and by analysing a number of Network-Area Relationships across different systems. In chapter 4, I used a subset of the empirical data to be able to constraint the sources of variation among the datasets and, thus, explore the determinants of the shape of NARs. The strong correlations between the spatial scaling of species richness with all network complexity properties, indicated that in this case, the main determinant of the shape of NARs was the spatial scaling of species richness. Therefore, it did not allow me to directly explore environmental determinants of the shape of NARs, but instead I analysed the main determinants of the shape of SARs. I identified the spatial variability of mean annual temperature and the spatial clustering of habitat types as the main determinants of the spatial scaling of diversity across Europe.

As discussed in chapter 4, while these mechanisms affected the spatial scaling of network complexity only indirectly through the effect on the spatial scaling of species richness for the European data, environmental factors can directly affect network structure across spatial scales. For instance, habitat loss or modification can alter species interactions [205], [206], [209] and the functions they perform [11], [207], [272], without large variations in species richness. Similarly, landscape heterogeneity can generate species sorting and priority effects, which can generate compartments in the community and promote a modular or compartmented network structure regardless of species richness [200], [201].

To progress on our understanding of NARs it is thus fundamental to disentangle the effect of species richness on the spatial scaling of all other network properties across different systems and biomes. Equally important is to determine the effect of other biotic and abiotic factors on the

shape of NARs, as it has been systematically studied for SARs. Particularly relevant is to explicitly analyse the effects of habitat heterogeneity on the spatial scaling of network modularity.

Scale invariance in ecological networks

Ecological network research has looked for universalities in the way species interact across different types of systems [5]–[8]. That is, patterns in ecological communities, such as the predominance of weak interactions between consumers and resources [24], [25], that are observed universally across all communities analysed. However, much less is known about scale invariant patterns in ecological networks. A pattern is considered scale invariant when it is equally observed when looking at different subparts of the same system. For instance, Blüthgen and colleagues [282], suggested that the degree of specialization of a network is independent of its size (i.e. total number of plant and animal species) when link weight is accounted for, indicating that patterns for biotic specialization might be scale invariant. Yet, most network properties in ecological research have been described as scale dependent (i.e., they are expected to change with species richness) [100], [101].

In this thesis I focused on understanding the variation of network structure across spatial scales. While most network properties showed to be dependent on the spatial scale considered and on the species richness of the network, others showed strikingly constant patterns regardless of the spatial scale and species richness. Specifically, the proportion of species across trophic levels in food webs and the modular structure of networks regardless the interaction type. This would suggest that there are a number of fundamental units in ecosystems that are self-similar across spatial scales, and they correspond to the modular structure and the vertical organization of diversity. Further analyses are needed to determine whether these patterns are scale invariant and which are the mechanisms behind their invariability.

Spatial scale in ecological network studies

Along all chapters of the thesis, I showed how network structure changes across spatial scales and how these changes might be dependent on the system analysed. In chapter 1, for instance, I showed how network structure can change from local to regional spatial scales in opposite directions along the gradient of environmental constancy. Similarly, in chapter 3, I showed how the spatial scaling of network structure depends on the type of data analysed, being slower in islands. Yet, ecological network studies often fail to acknowledge the spatial scale at which networks of species interactions were empirically characterized. This impedes the correct

estimation of the causes of variation of network structure and precludes a meaningful comparison between studies. If, as demonstrated in this thesis, network structure varies across spatial scales, then network studies estimating the causes of variation in network structure along environmental gradients [77], [174], [175] or between different types of systems, should systematically incorporate the spatial scale of observation.

As mentioned before, and in agreement with previous studies, part of the variability observed in the spatial scaling of network properties disappeared when controlling by species richness [99]–[102], especially for those properties describing the complexity of the community. However, I showed that properties related to the vertical diversity of the community, such as the proportion of species per trophic level, are difficult to predict solely from species richness. They did not show a consistent trend across systems suggesting that they might be differently affected by different spatial processes. While better understanding the role of species richness for all network properties remains a fundamental challenge to further disentangle the intrinsic role of the spatial scale of observation, my results suggest that controlling for species richness would account for most of the variation in network complexity, and hence it would suffice in comparative studies, but it would not explain all the variation observed in vertical diversity properties. Therefore, incorporating the spatial scale of sampling in comparative studies would provide additional key information on certain network properties and can also elucidate the processes behind structuring ecological communities.

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TITLE:

MACROECOLOGICAL NETWORKS: INTEGRATING BIOGEOGRAPHY, SPATIAL PROCESSES AND SPECIES
INTERACTION NETWORKS

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SUMMARY:

Research on ecological networks has identified universal patterns in the way species interact across different habitat types and their consequences for community dynamics and stability. However, most processes responsible for the observed structural patterns are suggested to operate at the local scale. The influence of processes operating at larger scales, such as climate or habitat heterogeneity, on the structure of species interaction networks, is still largely unknown. The main objective of this thesis is to build a comprehensive view on macroecological networks that integrates ecological networks and biogeography. First, I show how the geographical variation of the network structure depends on the spatial scale of observation. I then study theoretically and test empirically the mechanisms underlying changes in network structure across spatial scales and how these mechanisms vary across large biogeographical gradients. Thus, this thesis shows that understanding how the structure of ecological networks change with area size is central to assess the possible effects of habitat loss and fragmentation on ecological communities in a changing world.

KEYWORDS:

Biogeography, ecological networks, spatial scale, spatial processes, network structure, environmental gradients.

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RÉSEAUX MACROÉCOLOGIQUES: INTÉGRATION DE LA BIOGÉOGRAPHIE, DES PROCESSUS SPATIAUX ET DES
RÉSEAUX TROPHIQUES

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RÉSUMÉ :

La recherche sur les réseaux écologiques a identifié des motifs universels dans la façon dont les espèces interagissent entre elles. Les processus responsables de ces structures ont été étudiés à l'échelle locale. En revanche, l'influence de processus opérant à plus grande échelle, tels que le climat ou l'hétérogénéité des habitats, est encore très mal comprise. L'objectif principal de cette thèse est d'élaborer une vision globale des réseaux macroécologiques, intégrant réseaux écologiques et biogéographie. Dans un premier temps, je montre que la variation géographique de la structure des réseaux écologiques dépend de l'échelle spatiale d'observation. J'étudie ensuite de manière théorique et empirique les mécanismes qui sous-tendent le changement de structure des réseaux à travers les échelles spatiales et comment ces mécanismes varient à travers des gradients biogéographiques. Dans un monde en pleine mutation anthropogène, comprendre comment la structure de ces réseaux change avec l'aire des régions considérées est essentiel pour appréhender les conséquences écologiques de la perte d'habitat et de la fragmentation.

MOTS-CLÉS :

Biogéographie, réseaux trophiques, échelle spatiale, processus spatiaux, structure du réseaux, gradients de l'environnement

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