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## Invasion biology of ants under climate change

Cleo Bertelsmeier

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**ÉCOLE DOCTORALE : *Sciences du Végétal (ED 145)***  
**Laboratoire de *Ecologie, Systématique & Evolution (ESE)***

Discipline : Ecologie

**THÈSE DE DOCTORAT**

soutenue le 18/12/2013

par

**Cleo BERTELSMEIER**

**Biologie des invasions de fourmis dans un  
contexte de changement climatique**



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***“It has been said that the primary function of schools is to impart enough facts to make children stop asking questions. Those with whom the schools do not succeed become scientists.”***

***Knut Schmidt-Nielsen (physiologist, 1915-2007), “The Camel’s Nose”***

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*Für meine Allersüßesten: Mama, Papa, Mialí\*  
und meine Omas*

*\*Ohií, Papaloffski und der dritte Mann.*



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# General Introduction

# 1. INTRODUCTION

## 1.1. Biodiversity crisis

Global biodiversity is currently facing a crisis, which has been called the 6th mass extinction in the history of the Earth<sup>1</sup>. Extinction as such is a natural process: species evolve, diversify and go extinct. The mean lifetime of a species is approximately one million years in mammals and between 5 and 10 million years in invertebrates<sup>2</sup>. These “background extinctions” can be estimated from the fossil record. However, the current rate of species extinctions is about two orders of magnitude higher than the normal rate of extinctions<sup>3</sup> and projected rates of extinction by the end of the century could be 10 times higher than the current rate<sup>4</sup> (MA, Fig. 1).

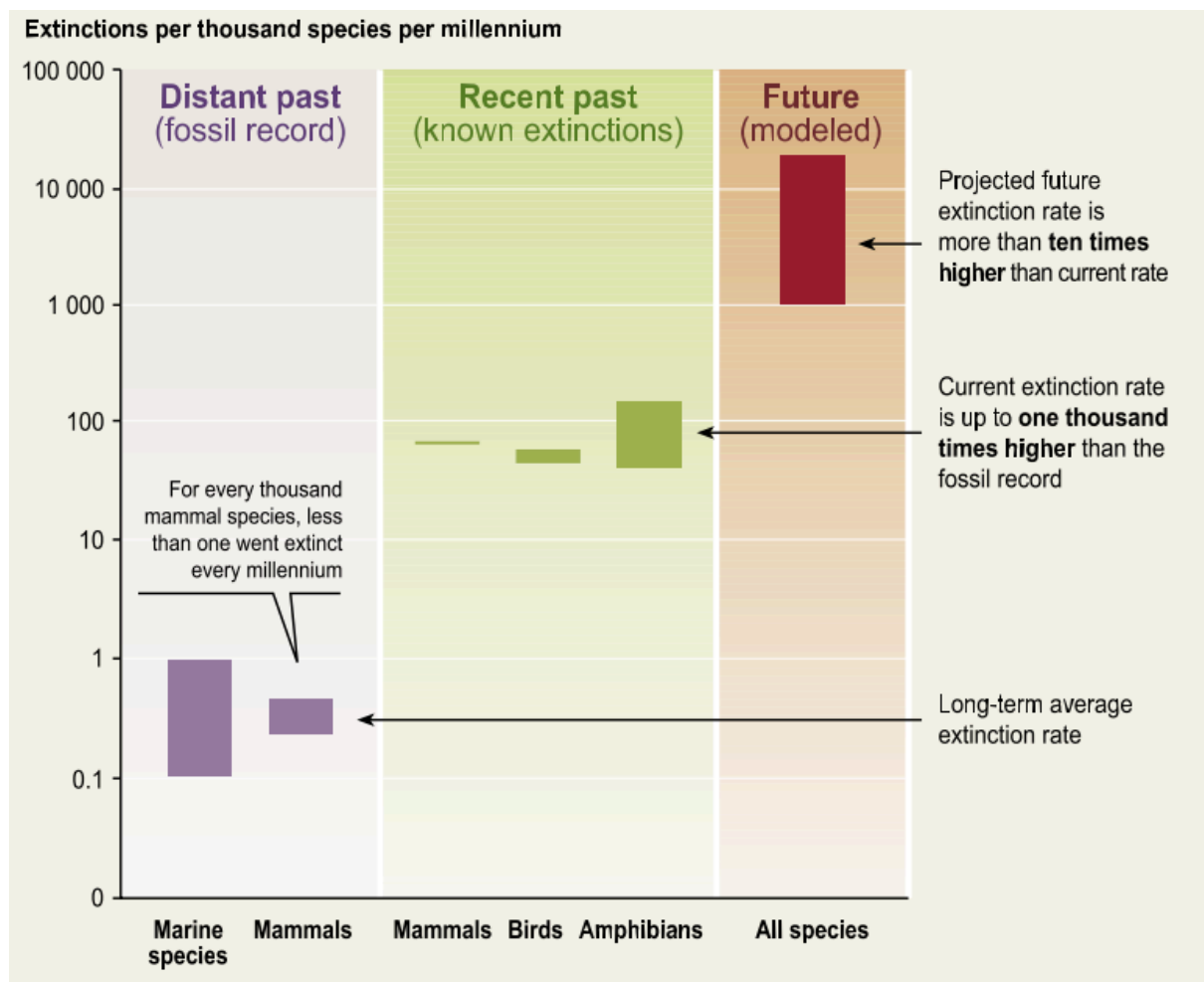


Fig. 1 Millennium Ecosystem Assessment: “ ‘Distant past’ refers to average extinction rates as estimated from the fossil record. “Recent past” refers to extinction rates calculated from known extinctions of species (lower estimate) or known extinctions plus “possibly extinct” species (upper bound). A species is considered to be “possibly extinct” if it is believed by experts to be extinct but extensive surveys have not yet been undertaken to confirm its disappearance. “Future” extinctions are model-derived estimates using a variety of techniques, including species-area models, rates at which species are shifting to increasingly more threatened

categories, extinction probabilities associated with the IUCN categories of threat, impacts of projected habitat loss on species currently threatened with habitat loss, and correlation of species loss with energy consumption. The time frame and species groups involved differ among the “future” estimates, but in general refer to either future loss of species based on the level of threat that exists today or current and future loss of species as a result of habitat changes taking place over the period of roughly 1970 to 2050. Estimates based on the fossil record are low certainty; lower-bound estimates for known extinctions are high certainty and upper-bound estimates are medium certainty; lower-bound estimates for modeled extinctions are low certainty and upper-bound estimates are speculative. The rate of known extinctions of species in the past century is roughly 50–500 times greater than the extinction rate calculated from the fossil record of 0.1–1 extinctions per 1,000 species per 1,000 years. The rate is up to 1,000 times higher than the background extinction rates if possibly extinct species are included.”<sup>4</sup>

The International Union for the Conservation of Nature (IUCN) estimates that currently, one-third of all amphibian species, one-fourth of all mammals and more than one in ten birds are sliding towards extinction<sup>5</sup>. But actual numbers may be much higher, because experts have evaluated so far only 43% of vertebrate species, 4% of plant species, and less than 0.5% of invertebrates<sup>5</sup>, meaning that others could be endangered, too. Particularly small or rare species, which are difficult to detect, could fall into this category. For example, among insects, most species have not even been described yet, let alone assessed regarding their extinction risks. Many of these species are likely to go extinct, without been known to science<sup>6</sup>.

## *1.2. Drivers of species extinctions*

The current biodiversity crisis has multiple causes, linked to human activities. Five main drivers of species extinctions have been identified (Fig. 2). In terrestrial ecosystems, changes in land cover have been the most important cause of extinctions over the last century, followed by species invasions, pollution, overexploitation and climate change. However, the future impacts are predicted to increase more for some drivers of species extinctions than others, depending on the ecosystems. Climate change and pollution are truly global threats, increasing in importance across all ecosystems<sup>4</sup>. Biological invasions are predicted to increase very rapidly in temperate and tropical forests, Mediterranean and tropical drylands, in inland waters and coastal regions<sup>4</sup>. Although invasive species are not predicted to increase on islands, they will continue to have devastating impacts, given that they are already a leading cause of species extinctions on islands today<sup>4</sup>.

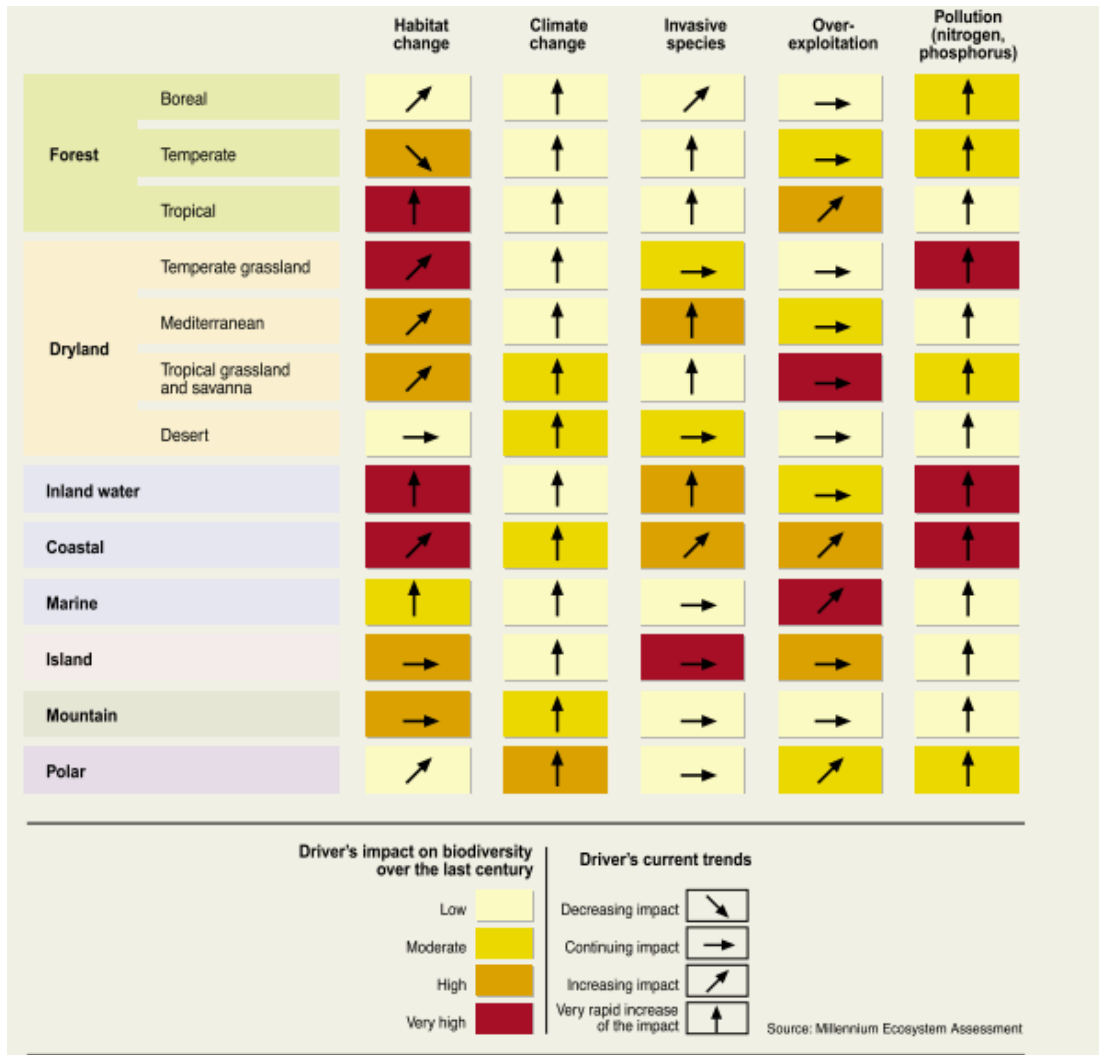


Fig. 2 Millennium Assessment: “The cell color indicates impact of each driver on biodiversity in each type of ecosystem over the past 50–100 years. High impact means that over the last century the particular driver has significantly altered biodiversity in that biome; low impact indicates that it has had little influence on biodiversity in the biome. The arrows indicate the trend in the driver. Horizontal arrows indicate a continuation of the current level of impact; diagonal and vertical arrows indicate progressively increasing trends in impact. Thus, for example, if an ecosystem had experienced a very high impact of a particular driver in the past century (such as the impact of invasive species on islands), a horizontal arrow indicates that this very high impact is likely to continue.”<sup>4</sup>

However, these drivers of species extinctions do not act in isolation and in fact, the greatest threat could stem from synergies between different drivers.

In this thesis, I was interested in the interaction between climate change and biological invasions. In the first chapters, I will present a review on the impacts of climate change on biodiversity (Chapter 2) and give a brief introduction about invasive species with a particular focus on the “100 of the worst invasive species” list (Chapter 3).

Climate change and biological invasions could act synergistically because the distribution of many invasive species is currently restricted by thermal barriers (too low temperatures) and climate change might enable them to invade higher latitudes. The

view that climate change will exacerbate invasions has become a widespread dogma in global change biology<sup>7-9</sup>. Theoretical frameworks have been developed explaining *how* climate change might re-enforce invasions and it has been widely discussed what will be the *consequences* of climate change-aided invasions<sup>10</sup>. Surprisingly, given the importance of the subject, this dogma remains poorly tested and theoretical arguments why biological invasions may *not* benefit from climate change are lacking. On the other hand, impacts of climate change on biodiversity are widely studied (see our review in Chapter 2) and arguments are not only based on imagined (theoretical) ways in which species might suffer from climate change. First, empirical observations have allowed to link species responses to climate change and second, a high number of studies have modelled species distributions under current and future climatic conditions, linking models with metrics of extinction risk (Chapter 2). Several global, taxon-wide assessments have been made to estimate the percentage of species likely to go extinct because of climate change. However, to my knowledge, no global, taxon-wide assessment has been made on the impact of climate change on invasive species. To me, this lack of studies combined with the strong affirmative nature of the ‘synergy dogma’ is very surprising, as I can see no convincing theoretical reason why invasive species should systematically benefit from climate change, whereas native species should systematically suffer from climate change.

My thesis is about forecasting the future of biological invasions under climate change. As a model system, I studied ants (*Formicidae*), which I will describe in more detail in Chapter 4 (Fig. 3).

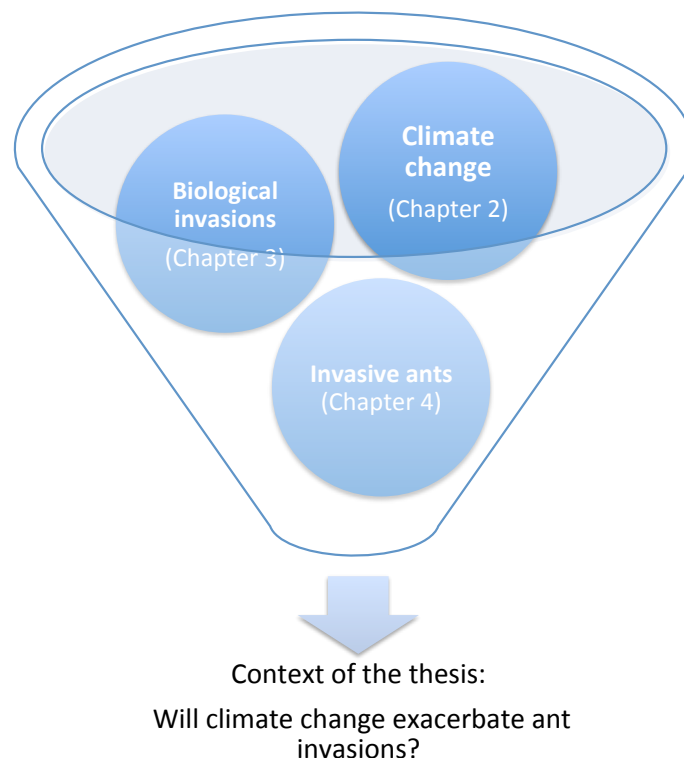


Fig. 3 The three ‘ingredients’ that describe the context of the thesis: Impacts of climate change on biological invasions, with invasive ants as a model system. The first chapters (2-4) will serve as a more general introduction and describe each of these three aspects separately. The following chapters will include primary research manuscripts.



### 1.3. Ants as a model system

Ants are an ideal model system for ecology and evolution<sup>11</sup>. There are more than 12,500 described species of ants<sup>12</sup> present on all continents but Antarctica but probably many more remain to be discovered and described<sup>13</sup>. They have colonized almost all terrestrial habitats, ranging from tropical forests to deserts, tundra, savannah, urban areas or agricultural landscapes<sup>14</sup>. Ants have a variety of lifestyles. Some species nest in trees, in the soil, the leaf litter, above ground, others construct large nest mounds and some are nomads. Their diet is equally varied, there are predators, scavengers, seed harvesters, exploiters of sugary exudates and omnivores<sup>11</sup>. Colony size varies hugely from less than 10 individuals to millions of workers (e.g. army ants). All ant species share a colonial lifestyle, where workers have given up reproduction in order to help raise the brood and take care of the queen(s). As a consequence of this hugely successful life-style, ants are dominant members of many ecosystems and have been called “key stone” species, because they influence many ecosystem functions, such as seed dispersal or soil chemistry<sup>15</sup>. Overall, their biomass is estimated to exceed the biomass of all other mammals combined and they account for up to 25% of terrestrial biomass<sup>16</sup>.

Ants are easily transported by humans because of their small sizes and nesting habits. Many species nest in superficial or ephemeral sites such as root masses, leaf litter, logs and in plant debris<sup>17</sup>. Exotic ants, which are intercepted at ports of entry<sup>18,19</sup>, are frequently detected on plant material (Fig 4). In total, over 200 species have established populations outside their native range<sup>17</sup> but it has been estimated that more than 600 species have already been introduced outside of their native range<sup>20</sup>. A small subset has become ‘invasive’, *i.e.* their establishment has been followed by a subsequent proliferation and expansion, leading to negative impacts on native biodiversity and/or human health<sup>21-23</sup>.

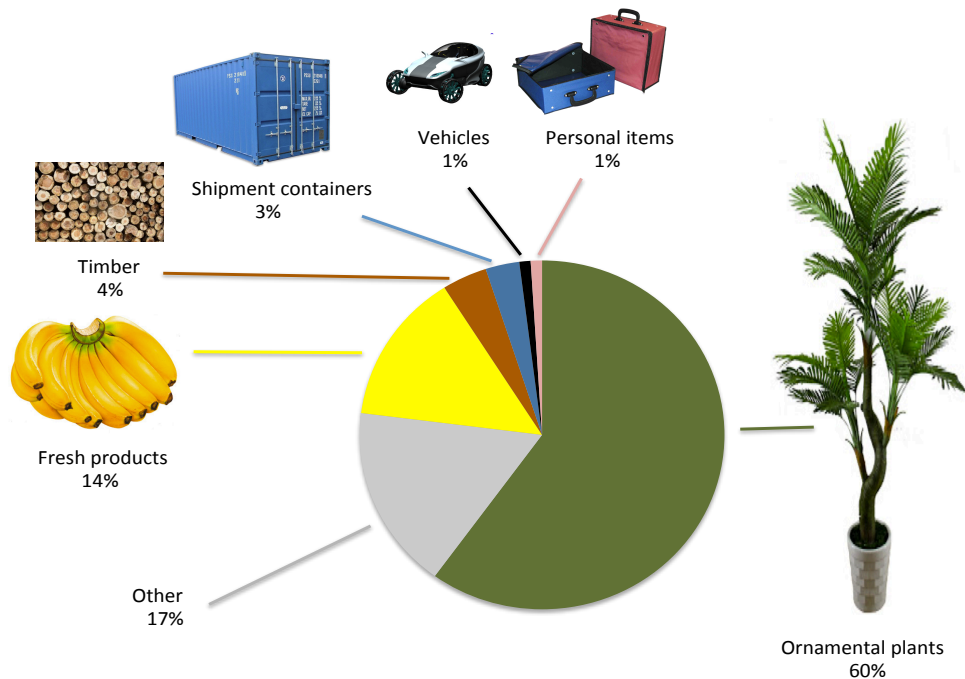


Fig. 4 Commerce on which ants are transported to the United states (Data from Suarez et al.<sup>19</sup>).

Currently the IUCN Invasive Species Specialist Group<sup>24</sup> recognizes 19 ant species as highly problematic and five species are even on the ‘100 of the worst invasive species’ list<sup>25</sup>: the Argentine ant (*Linepithema humile*), the yellow crazy ant (*Anoplolepis gracilipes*), the electric ant (*Wasmannia auropunctata*), the red imported fire ant (*Solenopsis invicta*) and the big-headed ant (*Pheidole megacephala*). Invasive ants are prominent among invasive species because of their enormous impacts on native biodiversity (see our review in Chapter 4). They reduce native ant diversity, displace other arthropods and affect negatively many vertebrate populations<sup>22</sup>. This leads to impacts on ecosystem function (e.g. seed dispersal, soil chemistry)<sup>22</sup>. In addition, invasive ants can damage electrical equipment, invade houses, and sometimes sting and cause anaphylactic shock, which can be fatal or transmit diseases<sup>24,26</sup>. In addition, they may be a nuisance in agricultural areas and reduce production. Overall, invasive ants can be economically costly<sup>27,28</sup>.

Because ants are extremely difficult to control once they have invaded an extensive area, it is preferable to prevent ant invasions or to eradicate the population when it is still relatively small<sup>29,30</sup>. Forecasting potential ant invasions is important in this context, as it might allow prioritizing certain species or certain areas.

Previous work on invasive ants has concentrated on only two species: *L. humile* and *S. invicta* (fig. 5), despite the enormous impacts caused by all of the highly invasive ant species. The objective of this thesis is to develop a predictive framework of ant invasions in general, especially in the light of on-going climate change and to test the dogma of the synergy between climate change and biological invasions.

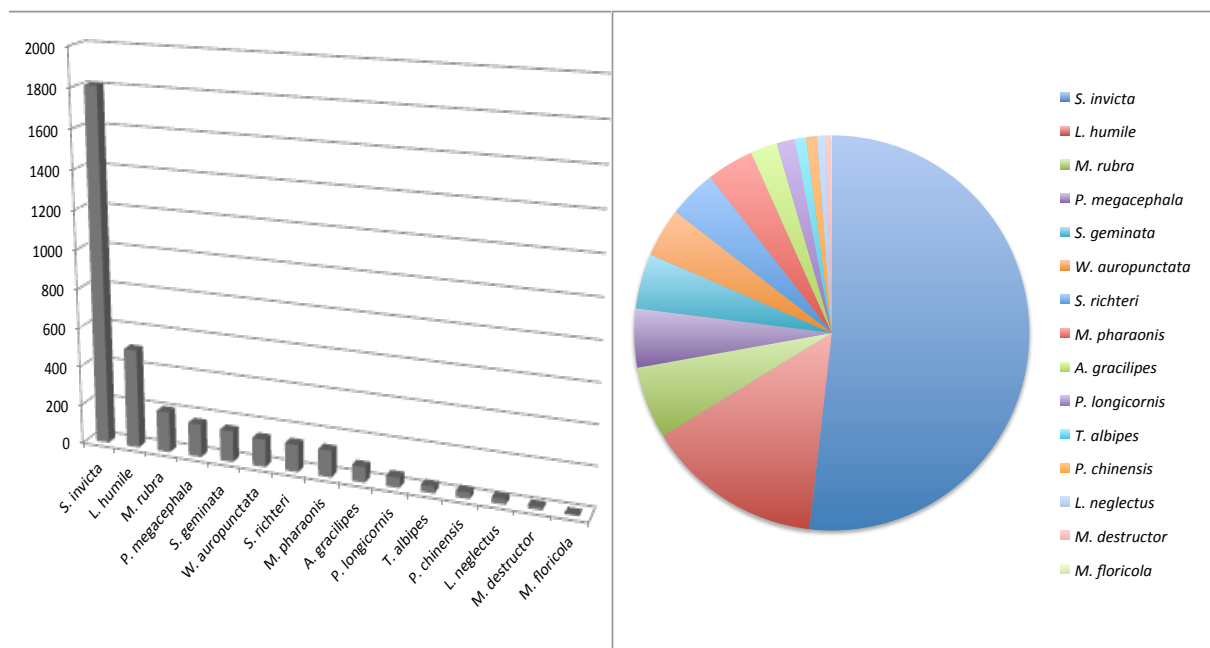


Fig. 5 Publications on invasive ants on ISI web of Science on 01 August 2012

#### 1.4. Approaches to predict ant invasions

In order to forecast ant invasions, I used three complementary approaches: mathematical modelling, lab and field experiments and the analysis of a database with ecological traits (Fig. 6).

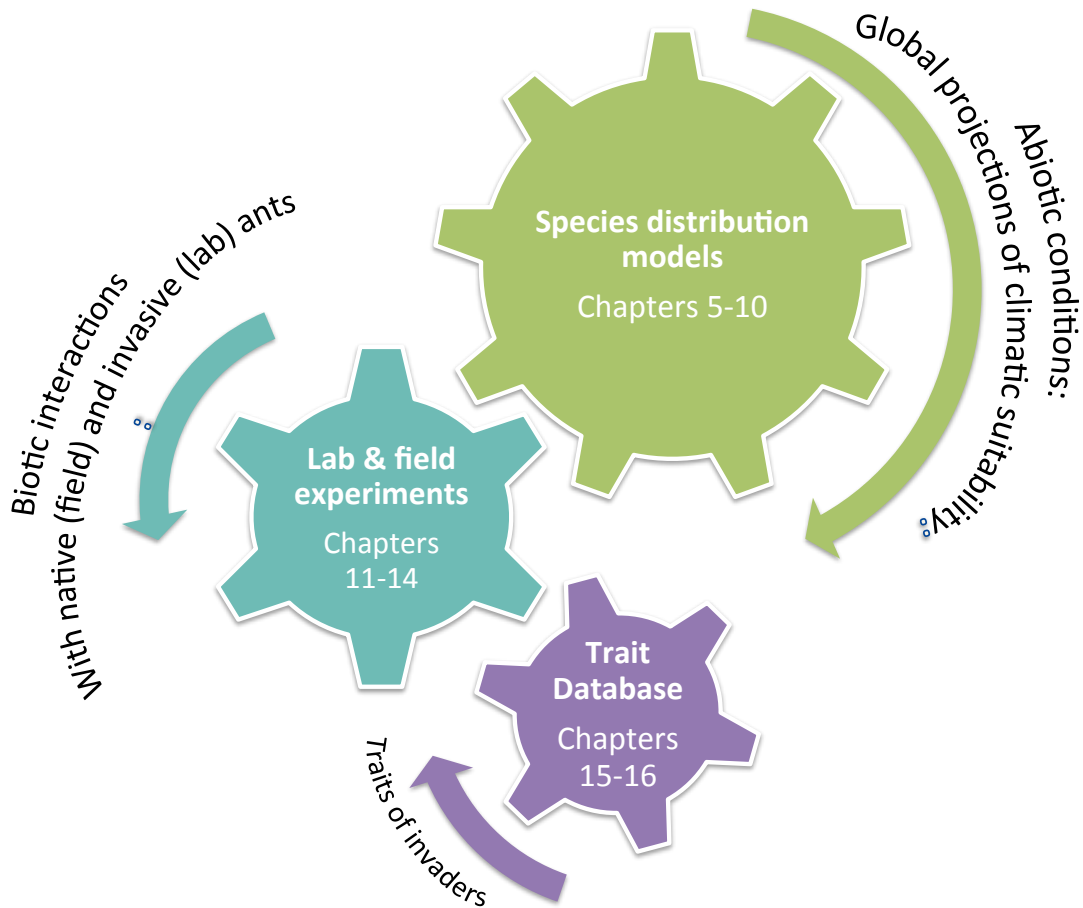


Fig. 6 Predicting future ant invasions

**Species distribution** models become increasingly widespread as a tool to forecast the future of biodiversity (Chapter 2). One of the greatest advantages of this method is that it requires only species occurrence data as input and can deliver useful approximations of favourable environmental conditions for a species. The underlying assumption is that a species' current distribution reflects its ideal climatic conditions. As a first step, the species occurrence data is mapped and each occurrence point is matched with a set of climatic variables (e.g. mean annual temperature, rainfall of the wettest month etc). Then, a certain algorithm is chosen to describe the relationship between a species' current distribution and the climatic data. This relationship (model) can then be projected on maps of current or future climates to identify areas of suitable climatic conditions(Fig.7).

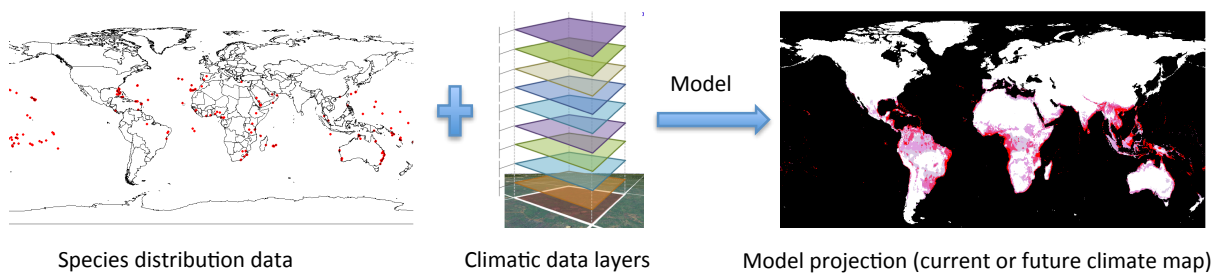


Fig. 7

However, a certain model projection in the future is contingent on the choice of the algorithm used and the future climate data. Future climate scenarios are produced by large climatic modelling centres in the form of Global Circulation Models (GCMs). There are around 20 different GCMs, which are all based on different geophysical assumptions. Data on different human development scenarios (CO<sub>2</sub> emission) are ‘injected’ in each of the GCMs to produce scenarios of future climate. According to the choice of algorithm, GCM and CO<sub>2</sub> emission scenario, the model output will be different. To circumvent this problem, I used several algorithms, GCMs and CO<sub>2</sub> emission scenarios and I combined their outputs in a consensual forecast (Fig 8).

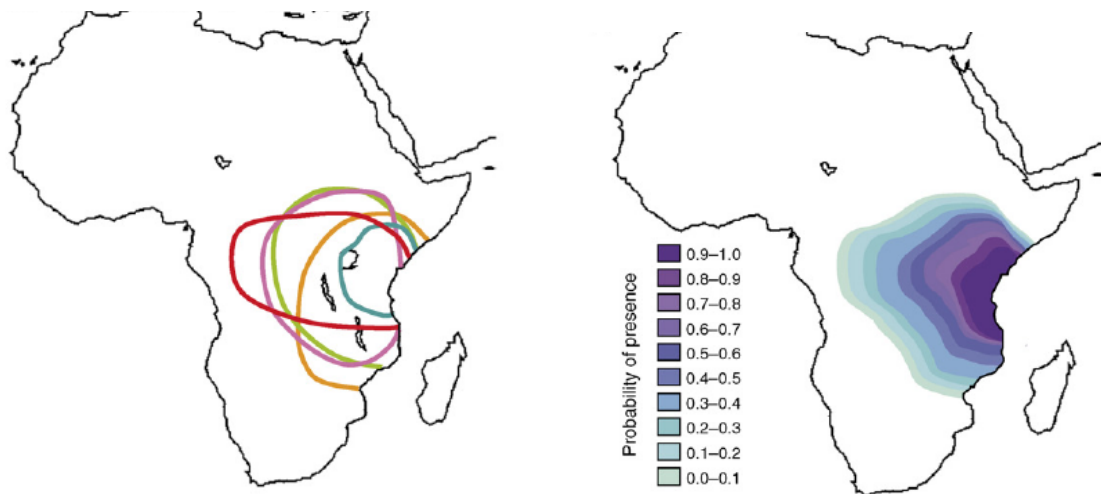


Fig. 8 Left: Outputs of individual models based on different combinations of algorithm x GCM x SRES. Right: Consensus model (Figure from Araujo&New 2007<sup>31</sup>).

Because species distribution models map only suitable climatic conditions but do not take into account biotic interactions, I complemented the modelling studies with experiments. First, I tested whether actual survival of the Argentine ant (*L. humile*) in the field is consistent with my model predictions. To this aim, I took part in a field study using an innovative experimental device that allows implementing artificial colonies in the soil and testing their survival in the field (Chapter 12). The artificial nest boxes are covered with a thin metal mesh that confines the queens to the interior of the box and allows only the sterile workers to forage outside (Fig. 9)



Fig. 9 Experimental nest, before being covered and buried in the soil.

As the models indicated overlapping suitable areas for different invasive ant species, I was interested in the interactions between those species and in predicting which would be the “top” dominant species. I realized dyadic confrontation experiments between seven highly invasive species, which may share climatically favourable areas. Because species can differ in their behaviour and fighting strategy depending on the group size, I realized worker-worker confrontations (allowing to record precisely the behaviour of the opponents) and group confrontations with 10 vs 10 workers (allowing to observe different group strategies) (Fig 10). In addition, I carried out observations at the colony level, connecting two colonies of different species and observing them over 6 weeks. Because behavioural dominance is not the only aspect of interspecific competition, I also tested the species abilities in exploring a new territory and discovering resources, as well as exploiting them, once they have been discovered. I used two different experimental devices, one to test exploitation, with different baits placed near the entrance of the colony. The other device was a complex maze that the ants needed to explore in order to find the bait, after several hours.

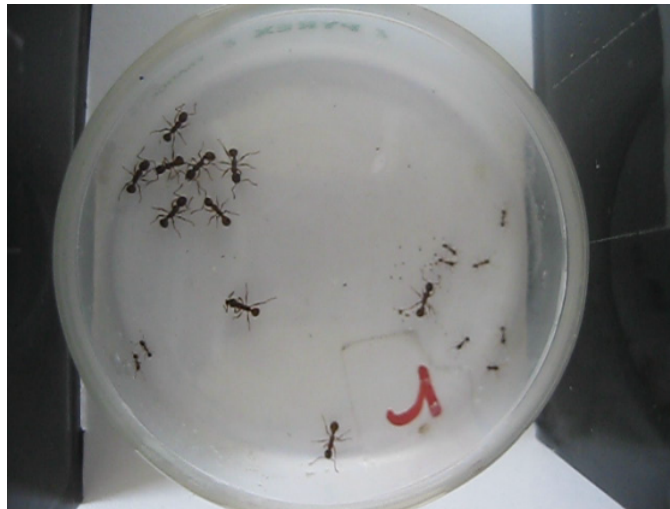


Fig. 10 Group confrontation

The combined approaches of species distribution models allow predicting where the most invasive ant species are likely to find suitable conditions and which species is likely to dominate, potentially displacing the other invasive ants from areas where they may invade simultaneously. However, these approaches give no indication about future ‘emerging’ invaders, i.e. species which are currently not invasive but may become so in the future (a recent example of a ‘new’ invasive ant species is *Pachycondyla chinensis*, the Asian needle ant, which has been added to the IUCN invasive species database last year). With the objective to characterize in a quantitative way the ‘profile’ of a typical invasive ant, I constructed an online database with 25 ecological traits and collected data on more than 2200 species of ants, in order to compare native and invasive ants worldwide.

The combination of the three approaches (models, experiments, database) allowed to investigate complementary aspects of the future of ant invasions and to investigate abiotic and biotic factors determining future invasions as well as species traits that could be used to identify future potential invasive species.

### 1.5. Thesis outline

#### PART 1: Study context

**Chapter 2** is a review on the impacts of climate change on biodiversity. The first part discusses different possible effects of climate change at the individual, population, species, ecosystem and biome scale, notably showing that a species can shift their climatic niche along three non-exclusive axes: time (e.g. phenology), space (e.g. distribution) and self (e.g. physiology). Failing to adapt long any of these axes, a species faces extinction. The second part of the review is about the most common approaches used to forecast the future of biodiversity at global and continental scales.

**Chapter 3** is an article that I co-authored, describing the selection of a new '100th' species for the list of the '100 of the worst invasive species' list by the IUCN, following the eradication of the rinderpest virus.

**Chapter 4** is a review on invasive ants. I summarize the impacts of invasive and discusses the difficulties in assessing them. The second part is about the keys of invasion success, including species traits, abiotic conditions, disturbance and human impacts, biotic interactions and geographic patterns and introduction pathways. The third part reviews possibilities to eradicate or to prevent ant invasions, including predictive models.

#### PART 2: Species distribution models

Chapters 5-10 use species distribution models to make spatial predictions for highly invasive ants under current and future climatic conditions.

**Chapter 5** shows a potential range expansion of a 'new' invasive species, the Asian needle ant, *Pachycondyla chinensis*.

**Chapter 6** is about potential increases in suitable areas for two invasive ant species, the destroyer ant, *Monomorium destructor* and the European fire ant, *Myrmica rubra*. In addition to the classic binary classification of areas as 'suitable' or 'unsuitable', I devised a climatic suitability index, through which I could determine variations in quality of potential habitat within a 'climatically favourable' area. In this study, both species were likely to benefit from climate change, but not in the same way. For one species, the 'quantity' of suitable habitat increase, for the other the 'quality' of suitable habitat improved.

**Chapter 7** is about the decrease in suitable areas for the big-headed ant, *Pheidole megacephala*, reaching a projected global loss of 19.4% of areas with a favourable climate by 2080. This decrease was observable in all continents and across all time horizons considered. These findings contradict the idea that invasive species will generally benefit from climate change.

**Chapter 8** is an assessment of potential suitable areas for 15 of the worst invasive ant species, both currently and with predicted climate change, globally, regionally and within the world's 34 biodiversity hotspots. I tested whether climate change and ant invasions systematically act synergistically.

**Chapter 9** assesses climatically suitable areas for 14 invasive ant species in France. Here, I focused on a region, instead of a species and mapped potential invasion hotspots in France under current and future climatic conditions. In addition, I investigated the climatic suitability for all 14 species at the departmental level and at the main ports of entry. I provide a ranking of risk per species for 17 major airports and 14 maritime ports.

**Chapter 10** explores whether the choice of the target horizon in the future can influence qualitatively the conclusions based on species distribution models. The results indicate that for 6 out of 15 species modelled, the trend of potential habitat size (i.e. decrease or increase) changed over time. In four species, the sign of the trend changed, from an initial expansion to a subsequent reduction or vice versa, depending on the date projected to. These findings stress the importance of using several projection horizons to avoid misled species management decisions.

### *PART 3: Experiments*

Chapters 11-14 take an experimental approach to investigate biotic interactions.

**Chapter 11** is a study, which combines a modelling approach of the potential suitable areas for Argentine ants in Europe with a field-based approach testing experimentally the species' potential to invade under different climatic conditions, in Spain along the front of a current invasion and in France, where models predict impossibility to invade. Ant colonies were placed in secure artificial nests that confined the queens to the interior and allowed the workers to pass through a metal grid and to forage outside. My contribution in this study was the modelling part and I also helped during the field experiments.

In **Chapter 12** I explore interactions among highly invasive ant species, which have been shown to have overlapping suitable areas (Chapter 8 and 9). Each of the species included in this study is capable of becoming numerically and behaviourally dominant and of displacing native species. However, it remains to be investigated which species would be behaviourally dominant when confronted with another invasive ant species, should two species be introduced in the same area. The aim of this study was to evaluate the performance in interference competition of the 7 of the world's worst invasive ant species in pairwise confrontations, testing the behaviour of each species against each of the 6 other species (in total 21 dyadic confrontations). I used single worker confrontations and group interactions of 10 vs 10 individuals to establish a dominance hierarchy among invasive ant species and I identified two different behavioural 'strategies'.

**Chapter 13** is about interactions among invasive ants at the colony level. These interactions were recorded at a daily basis over 6 weeks and the demography of interacting colonies was analysed. Overall, this dominance hierarchy is consistent with the results found in classical petri-dish interference interactions between small groups of workers. However, the results demonstrated more complex dynamics, rendering the outcome of pairwise species interactions less predictable.

**Chapter 14** is about the resource exploitation and exploration capacities in invasive ants. Invasive ants are thought to be at the same time behaviourally dominant and fast discoverers of resources, compared to native species. However, it has not yet been

tested whether such a trade-off exists among invasive ants, which may be able to arrive and establish in the same areas in the future. I designed two experiments to test the species' capacity to explore a maze, where a food resource has been located, and the capacity to exploit the food resources. Subsequently, I compared the discovery/exploitation ability with the previously established behavioural dominance hierarchy (Chapter 12).

#### *PART 4: Trait database*

Chapters 15 and 16 are about the database Antprofiler and its use to identify potential characteristics of invasive ants.

**Chapter 15** is a descriptive article about the database I constructed on (24) ecological traits of ants worldwide, its content and what kind of ecological questions may be answered using the database.

**Chapter 16** is a quantitative comparison of the traits of native and invasive ants, using data for more than 2200 ant species worldwide. I identified 9 traits for which native and invasive ants showed significant differences.

**Chapter 17** is a general discussion, perspectives and conclusion of the thesis.

#### **Appendices**

**Appendix 1** is a short note about the selection of the new 100<sup>th</sup> of the '100 of the worst invasive species' – and is essentially a shorter version of Chapter 3.

**Appendix 2** is a study of the potential distribution of an exotic butterfly species and the availability of its host plant in Australia. I have carried out the modelling part of the study – using the same tools as in the studies on ants of the Part 2.

**Appendix 3** is a study about the diet preferences of invasive ants. Commonly it is assumed that different ants have preferences for certain types of food (e.g. protein, sugar...) but not that they differ in their preferences for different substances of the same category. This is why the choice of a sugary bait (honey, cookies...) is generally not discussed. Here, I show different preferences for different types of sweetened drinks in two invasive ant species. The implication of this study is that relative abundances of the species could be over- or underestimated in the field, depending on the type of bait that was used.

**Appendix 4** is a chapter of the Encyclopedia of Theoretical Ecology about the role of fundamental ecology for applied ecology, where we take research in climate change biology as an example.

**Appendix 5** is a popular science article on the impacts of climate change on biodiversity that I wrote for the French magazine "Revue de la découverte".

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# Impacts of climate change on the future of biodiversity

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\* equal contribution



## REVIEW AND SYNTHESSES

## Impacts of climate change on the future of biodiversity

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### Abstract

Many studies in recent years have investigated the effects of climate change on the future of biodiversity. In this review, we first examine the different possible effects of climate change that can operate at individual, population, species, community, ecosystem and biome scales, notably showing that species can respond to climate change challenges by shifting their climatic niche along three non-exclusive axes: time (e.g. phenology), space (e.g. range) and self (e.g. physiology). Then, we present the principal specificities and caveats of the most common approaches used to estimate future biodiversity at global and sub-continental scales and we synthesise their results. Finally, we highlight several challenges for future research both in theoretical and applied realms. Overall, our review shows that current estimates are very variable, depending on the method, taxonomic group, biodiversity loss metrics, spatial scales and time periods considered. Yet, the majority of models indicate alarming consequences for biodiversity, with the worst-case scenarios leading to extinction rates that would qualify as the sixth mass extinction in the history of the earth.

### Keywords

Biodiversity, climate change, species extinctions.

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### INTRODUCTION

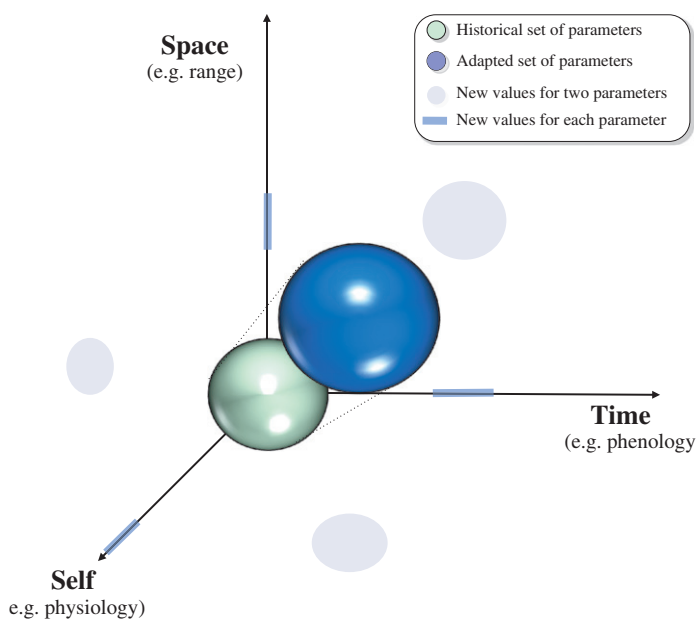
Predicting the response of biodiversity to climate change has become an extremely active field of research (e.g. Dillon *et al.* 2010; Gilman *et al.* 2010; Pereira *et al.* 2010; Salamin *et al.* 2010; Beaumont *et al.* 2011; Dawson *et al.* 2011; McMahon *et al.* 2011). Predictions play an important role in alerting scientists and decision makers to potential future risks, provide a means to bolster attribution of biological changes to climate change and can support the development of proactive strategies to reduce climate change impacts on biodiversity (Pereira *et al.* 2010; Parmesan *et al.* 2011). Although there is relatively limited evidence of current extinctions caused by climate change, studies suggest that climate change could surpass habitat destruction as the greatest global threat to biodiversity over the next few decades (Leadley *et al.* 2010). However, the multiplicity of approaches and the resulting variability in projections make it difficult to get a clear picture of the future of biodiversity under different scenarios of global climatic change (Pereira *et al.* 2010). Hence, there is an urgent need to review our current understanding of the effects of climate change on biodiversity and our capacity to project future impacts using models. To this end, we have reviewed both the ranges of possible impacts of climate change that operate at individual, population, species, community, ecosystem and biome scales and the different responses that could occur at individual, population or species levels. We then present the principal specificities and caveats of the most common approaches used to model future biodiversity at global and sub-continental scales and we synthesise their results focusing on how model combinations are used to project the impacts of climate change on species loss. Finally, we highlight several challenges for future research, from theoretical (e.g. emerging models) and applied (e.g. population conservation and exploitation) realms.

### BIODIVERSITY AND CLIMATE CHANGE: EFFECTS AND RESPONSES

#### Climate change effects on biodiversity

The multiple components of climate change are anticipated to affect all the levels of biodiversity, from organism to biome levels (Fig. 1, and reviewed in detail in, e.g. Parmesan 2006). They primarily concern various strengths and forms of fitness decrease, which are expressed at different levels, and have effects on individuals, populations, species, ecological networks and ecosystems. At the most basic level of biodiversity, climate change is able to decrease genetic diversity of populations due to directional selection and rapid migration, which could in turn affect ecosystem functioning and resilience (Botkin *et al.* 2007 but, see Meyers & Bull 2002). However, most studies are centred on impacts at higher organisational levels, and genetic effects of climate change have been explored only for a very small number of species.

Beyond this, the various effects on populations are likely to modify the 'web of interactions' at the community level (Gilman *et al.* 2010; Walther 2010). In essence, the response of some species to climate change may constitute an indirect impact on the species that depend on them. A study of 9650 interspecific systems, including pollinators and parasites, suggested that around 6300 species could disappear following the extinction of their associated species (Koh *et al.* 2004). In addition, for many species, the primary impact of climate change may be mediated through effects on synchrony with species' food and habitat requirements (see below). Climate change has led to phenological shifts in flowering plants and insect pollinators, causing mismatches between plant and pollinator populations that lead to the extinctions of both the plant and the pollinator with expected consequences on the structure of plant–pollinator networks (Kiers *et al.* 2010; Rafferty & Ives 2010). Other modifications of interspecific



**Figure 1** Summary of some of the predicted aspects of climate change and some examples of their likely effects on different levels of biodiversity.

relationships (with competitors, prey/predators, host/parasites or mutualists) also modify community structure and ecosystem functions (Lafferty 2009; Walther 2010; Yang & Rudolf 2010).

At a higher level of biodiversity, climate can induce changes in vegetation communities that are predicted to be large enough to affect biome integrity. The Millennium Ecosystem Assessment forecasts shifts for 5–20% of Earth's terrestrial ecosystems, in particular cool conifer forests, tundra, scrubland, savannahs and boreal forest (Sala *et al.* 2005). Of particular concern are 'tipping points' where ecosystem thresholds can lead to irreversible shifts in biomes (Leadley *et al.* 2010).

A recent analysis of potential future biome distributions in tropical South America suggests that large portions of Amazonian rainforest could be replaced by tropical savannahs (Lapola *et al.* 2009). At higher altitudes and latitudes, alpine and boreal forests are expected to expand northwards and shift their tree lines upwards at the expense of low stature tundra and alpine communities (Alo & Wang 2008). Increased temperature and decreased rainfall mean that some lakes, especially in Africa, might dry out (Campbell *et al.* 2009). Oceans are predicted to warm and become more acid, resulting in widespread degradation of tropical coral reefs (Hoegh-Guldberg *et al.* 2007). The implications of climate change for genetic and specific diversity have potentially strong implications for ecosystem services. The most extreme and irreversible form of fitness decrease is obviously species extinction. To avoid or mitigate these effects, biodiversity can respond in several ways, through several types of mechanisms.

### Biodiversity responses to climate change

Because of climate changes, species may no longer be adapted to the set of environmental conditions in a given region and could therefore fall outside its climatic niche. As other components of the ecological niche of species are not supposed to change directly, we will hereafter refer only to climatic niches of species (i.e. the climatic components of the *n*-dimensional hypervolume *sensu* Hutchinson). To persist, individuals, populations or species must produce adaptive responses,

which can be of several types, and are provided by two categories of mechanisms.

#### *Response mechanisms: plastic vs. genetic*

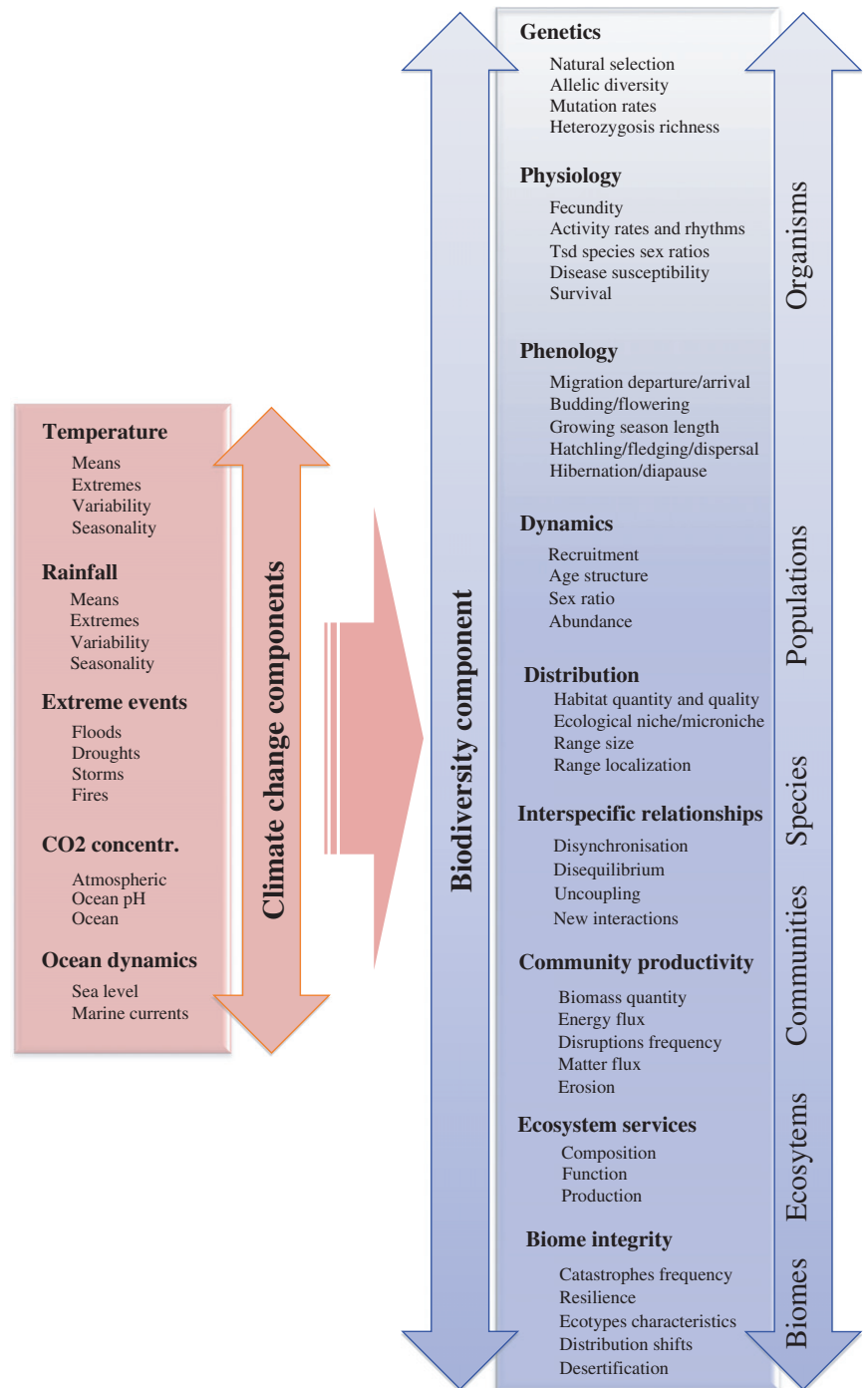
One of the crucial questions in the debate on ecological effects of climate change is whether or not species will be able to adapt fast enough to keep up with the rapid pace of changing climate (Lavergne *et al.* 2010; Salamin *et al.* 2010). Whatever the type of adaptive responses, underlying mechanisms are either due to micro-evolution (i.e. species can genetically adapt to new conditions through mutations or selection of existing genotypes Salamin *et al.* 2010) or plasticity, which provides a means of very short-term response (within individual's lifetimes, Charmanier *et al.* 2008). It may involve intraspecific variation in morphological, physiological or behavioural traits, which can occur on different time scales within the populations' spatial range (Botkin *et al.* 2007; Chevin *et al.* 2010). Empirical evidence suggests that plastic contribution is often more important than genetic contribution, as observed in birds and marmots (Hoffman & Sgro 2011). On the other hand, there is increasing empirical evidence that evolution can be very rapid (Lavergne *et al.* 2010). This is the case for many introduced species, for which selection-driven phenotypic changes have enhanced the invasive potential (e.g. Phillips 2009). Recent experiments on evolutionary rescue also confirm that rapid evolution through mutation and selection could allow species with rapid life cycles to adapt very severe and rapid environmental changes (Bell & Gonzalez 2009).

#### *Responses: along three axes*

Whatever the mechanisms involved in response to climate change, species can in theory change, and changes have already been observed, along three distinct but non-exclusive axes (Fig. 2): spatial, temporal or self. The first two axes correspond to easily observable and well documented responses to global warming (Parmesan 2006). 'Self' corresponds to less visible physiological and behavioural changes that allow species to adapt to the new climatic conditions in the same spatial and temporal frame.

*Spatial.* First, species can track appropriate conditions in space and follow them. This is typically done through dispersion, but spatial changes are not limited to this: shifts to a different habitat at the local or micro-habitat levels are also relevant. One of the best-documented responses – from both palaeontological records and recent observations – is a spatial shift of species tracking suitable climatic conditions at the regional scale. Latitudinal and altitudinal range shifts have already been observed in more than 1000 species – especially those with high dispersal capacities like birds, insects and marine invertebrates (Parmesan 2006), leading to a reduction in range size particularly in polar and mountaintop species (Forero-Medina *et al.* 2010). However, individuals shift their distribution to stay in quasi-equilibrium with the climatic conditions they are adapted to, but they may not be adapted to other abiotic variables such as photoperiod or novel biotic interactions (Visser 2008). In these cases, micro-evolution may be needed for them to persist (Visser 2008).

*Temporal.* To keep up with changing abiotic factors that show cyclic variation over time, such as temperature on a daily or yearly period, individuals can also respond to climate change through a shift in time (on a daily to seasonal basis). Phenology, i.e. the timing of life cycle events such as flowering, fruiting and seasonal migrations, is one of the most ubiquitous responses to 20th century climate warming. It has



**Figure 2** The three directions of responses to climate change through phenotypic plasticity or evolutionary responses : moving in space (dispersing to areas with suitable habitat or changing location on a microhabitat scale), shifting life history traits in time (adjusting life cycle events to match the new climatic conditions, including phenology and diurnal rhythms), or changing life history traits in its physiology to cope with new climatic conditions. Species can cope with climate change by shifting along one or several of these three axes.

already been documented in many species (Parmesan 2006; Charmantier *et al.* 2008). In a meta-analysis of a wide range of species including animals and plants, the mean response across all species responding to climate change was a shift in key phenological events of 5.1 days earlier per decade over the last 50 years (Root *et al.* 2003). Flowering has advanced by more than 10 days per decade in some species (Parmesan 2006). These phenological changes can help species keep synchrony with cyclical abiotic factors. Yet, they can also be disruptive, by increasing asynchrony in predator-prey and insect-plant systems (Parmesan 2006), which may lead to species extinction. Temporal shifts may also occur at a small temporal scale, e.g. with

behaviours or activity patterns adjusted in daily activity rhythms to match the energetic costs of a different climatic condition.

*Self.* Last, species can cope with changing climatic conditions by adapting themselves to the new conditions in their local range, rather than by tracking their current optimal conditions in space or time. For lack of a better term, we refer to these *in situ* changes that are not related to spatial or temporal changes, as changes in 'self'. Species can move along this third, 'self' axis by physiological alterations that allow tolerance to warmer or drier conditions or by behavioural modifications of their diet, activity and energy budget, for example. Although they are often less obvious than changes in time or space, some



physiological responses have already been reported (Johansen & Jones 2011) during the 20th century climate change, especially from many ectotherms, as their locomotion, growth, reproduction and sex determination are temperature sensitive (Tewksbury *et al.* 2008). However, for many traits, plastic phenotypic responses should reach a physiological limit and 'saturate' in extreme environments. For example, body size or metabolic rate cannot increase or decrease indefinitely under sustained environmental change (Chevin *et al.* 2010). In this case, strong selection is needed to cope with climate change. As they remain in the same spatial and temporal frame, thereby limiting alterations of interspecific relationships, changes in self also have different consequences for ecosystem responses than do changes in time and space.

Failing to adapt along one or several of these three axes, population or species will go extinct locally or globally. There is thus a multitude of possible responses for species to cope with climate change, and in fact relatively few taxa went extinct following climate change during the Quaternary period (Botkin *et al.* 2007). This should help temper catastrophist predictions regarding the global effects of the current climate change on biodiversity. However, the responses of many populations are likely to be inadequate to counter the speed and magnitude of the current climate change. In addition, unlike in past periods of climate change, species have now to cope with additional threats, some of which may act in synergy with climate change (Botkin *et al.* 2007). As we are already facing an irrefutable biodiversity crisis, the number of species that may go extinct following climate change has become a major concern over the last few years.

## ASSESSING THE FUTURE OF GLOBAL BIODIVERSITY

Our understanding of the effects of global climate change on biodiversity and its different levels of response is still insufficiently well developed. Yet, it is enough to raise serious concern for the future of biodiversity. The most pressing issue is to quantitatively assess the prospects for biological diversity in the face of global climate change. Although several methods exist to draw inferences, starting with existing palaeontological or recent data, experiments, observations and meta-analyses (e.g. Lepetz *et al.* 2009), ecological modelling is the most commonly used tool for predictive studies. Progress in this field is characterised by both an extremely high pace and a plurality of approaches. In particular, there are three main approaches to projecting species loss, concentrating either on future changes in species range or species extinction or changes in species abundance. However, all three modelling approaches have so far largely focused on one axis of response (change in space), largely overlooking the importance of the other aspects. In addition, they seldom account for the mechanisms of these responses (plasticity and evolution). We briefly discuss herein the basic principles and the weakness of the models that are the most widely used at global or at large regional scales in this context, focusing on representative examples of recent work. Table 1 summarises the specific advantages and limitation of each model type.

### Biodiversity range models components

Studies modelling species' range shifts are generally based on the assumption that species niches are defined by a small set of environmental variables, i.e. the species' 'climate niche', defines the suitable climatic habitat for that particular species. These Bioclimatic

Envelope Models relate current species ranges to multiple climatic variables and thereby define the climatic niche (envelope) for each species. It is then possible to project this niche for different future climate scenarios to determine the potential redistribution of the suitable climate space of the species. The extinction risks can then be calculated in different ways using species–area relationships (Thomas *et al.* 2004) or IUCN status (Thuiller *et al.* 2005). Despite a number of limitations (lack of biological process as well as methodological and theoretical issues, Soberon & Nakamura 2009), species distribution models still constitute the bulk of studies in this domain (Sinclair *et al.* 2010).

Shifts in distinct vegetation types, often referred to as biome or habitat shifts are often simulated with Dynamic Vegetation Models (DVM). These models forecast shifts in vegetation and associated biogeochemical and hydrological cycles in response to climate change. DVMs use time series of climate data (e.g. temperature, precipitation, humidity, sunshine days) and take into account constraints of topography and soil characteristics to simulate monthly or daily dynamics of ecosystem processes. Plant species are represented as groups with similar physiological and structural properties, termed Plant Functional Types (PFTs), which are designed to represent all major types of plants (Sitch *et al.* 2008). PFT distributions can then be used to estimate changes in biome or habitat ranges. Currently, DVMs are of limited use for projecting responses in biodiversity directly (i.e. the absence of animals and the limitation to *c.* 10 PFTs exclude direct utilisation). However, coupled with extinction models, they allow extinction risk for species to be estimated at the regional or global scale (e.g. van Vuuren *et al.* 2006).

### Species loss models components

The simplest method for calculating extinction risk is to assume that species go extinct when they no longer have any suitable habitat (Jetz *et al.* 2007). This may underestimate extinctions because species often enter an 'extinction vortex' well before they lose their entire habitat. Yet, it could also substantially overestimate extinctions because many species have weak habitat specificity (Malcolm *et al.* 2006; Willis & Bhagwat 2009).

The species–area relationship (SAR), an empirical relationship between the number of species and the land area of a region, is often used to estimate extinction risk (Thomas *et al.* 2004). Species extinctions are calculated as a direct function of habitat loss or climate-induced range contraction based on the observation that extinction risk increases with decreasing range and population size. SAR methods may over- or underestimate species extinction risk depending on the capacity of species to persist in small populations or adapt to novel environments, and they also fail to provide a time frame in which extinctions are likely to occur (Chevin *et al.* 2010) because the extinction debt is not accounted for (Pereira *et al.* 2010). The relevance of using this relationship to project biodiversity loss is still hotly debated (He & Hubbell 2011).

The IUCN has developed criteria to assess species extinction risk for their Red List of the conservation status of plant and animal species (Baillie *et al.* 2004). These include 90 biological traits identified as enhancing species' vulnerability (e.g. habitat specialisation, narrow environmental tolerance, dependence on specific environmental triggers, dependence on interspecific interactions or poor ability to disperse to or colonise a new range, Foden *et al.* 2008). Recent attempts at projecting climate change impacts on biodiversity have

**Table 1** Advantages and disadvantages of the two components of major modelling approaches used to estimate loss of biodiversity due to climate change. See Fig. 3 for illustrations of how the two components can be combined to estimate biodiversity loss

	Advantages	Disadvantages	Key references
<b>Biodiversity range model components</b>			
Bioclimatic envelope models (BEM)	Can be applied to a large number of species and a variety of taxonomic groups Implicitly capture many ecological processes in the relationship between occurrence data and spatial information Require few data	Do not explicitly account for mechanisms that mediate species range May handle novel climates poorly Lack temporal dynamics Assume that the current distribution of a species is a good indicator of suitable climate	Alo & Wang (2008), Araùjo <i>et al.</i> (2011), Baillie <i>et al.</i> (2004), Beaumont <i>et al.</i> (2008, 2011), Botkin <i>et al.</i> (2007), Bradley <i>et al.</i> (2010), Brook <i>et al.</i> (2008)
Dynamic vegetation models (DVMs)	Include the dynamics of plant growth, competition and, in a few cases, migration Allow the identification of future trends in ecosystem function and structure Can be used to explore feedbacks between biosphere and atmospheric processes	Require detailed physiological data Do not include plant interactions with other taxonomic groups Limit biodiversity to a very small number of plant functional types Do not take into account fine scale spatial heterogeneity Are not adapted for predicting species extinctions at local scales	Akçakaya <i>et al.</i> (2006), Anderson <i>et al.</i> (2009), Bakkenes <i>et al.</i> (2002), Brook <i>et al.</i> (2008, 2009), Campbell <i>et al.</i> (2009)
<b>Species loss model component</b>			
Species–area relationships (SAR)	Are easy to couple with distribution models because they are based on range or habitat loss Can be applied to a variety of taxonomic groups Require few data	Use values of key parameters that are not well constrained Lack empirical evidence concerning applicability of SAR for climate change or at species range level Lack temporal dynamics Don't account for processes influencing extinction rates (e.g. population dynamics, adaptive responses)	Alo & Wang (2008), Campbell <i>et al.</i> (2009), Carnaval <i>et al.</i> (2009), Charmantier <i>et al.</i> (2008)
IUCN status methods	Use a widely accepted measure of threat Are simple to couple with distribution models because partly based on criteria of range or habitat loss	Depend on thresholds that are somewhat arbitrary Rely on sole criteria of declining range size in most studies Often don't respect time frame for declines (i.e. 10 years or three generations in most cases)	Alo & Wang (2008), Araùjo <i>et al.</i> (2011), Chevin <i>et al.</i> (2010)
Dose–response relationships	Are anchored in measured responses of biodiversity to global change drivers Can assess the impact of a wide range of global change factors alone or their cumulative effects Can include time lags	'Undisturbed' ecosystems used as baseline are difficult to define Inadequately account for interactions between global change drivers Lack validation at large regional or global scales Use metrics that are difficult to relate to common biodiversity indices	Bakkenes <i>et al.</i> (2002), Barnosky <i>et al.</i> (2011)

used the IUCN status metric to obtain estimates of extinction rates based on projected range shifts (Thuiller *et al.* 2005), although the use of IUCN status for this purpose has also been questioned (Akçakaya *et al.* 2006).

In dose–response relationship (DRR) models, observational data and experiments can be employed to generate empirical relationships between the relative importance of global drivers (dose) and changes in species loss (response).

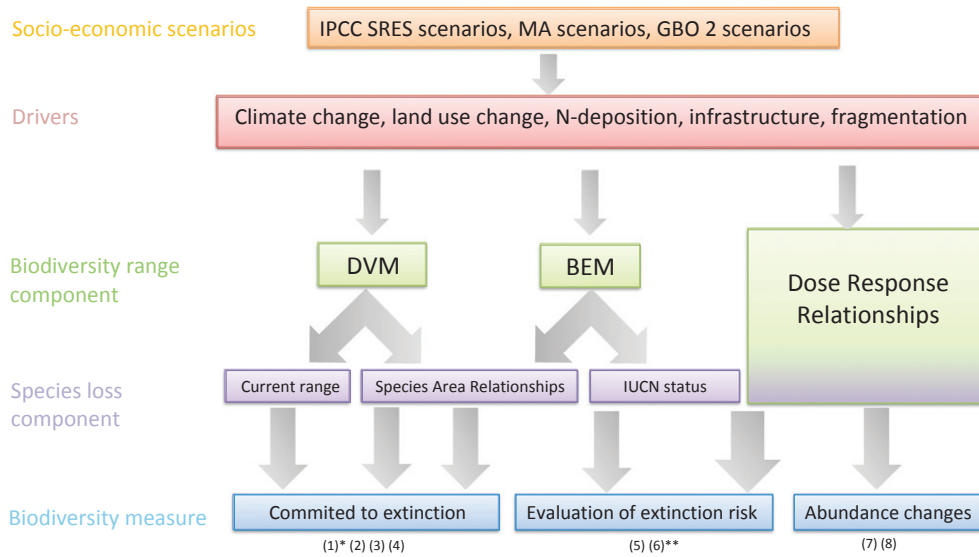
Most models focus on species extinctions, which are only the last step of a decline in abundance and are a less immediate (although dramatic) impact of climate change. This fact has led to the development of new models that attempt to quantify the impact of human activities on species abundance (i.e. an equivalent of DRR for species abundance). Impacts on biodiversity are estimated using biodiversity indicators including mean species abundance (MSA, Alkemade *et al.* 2009) and Biodiversity Intactness Index (Biggs *et al.* 2008). For example, the GLOBIO model uses a matrix of changes in mean local species abundances following conversion between two land use or land cover categories, derived from empirical

studies (Leadley *et al.* 2010). These types of models use species abundances in pristine ecosystems as a baseline, and thereby provide a measure of the distance from 'naturalness' of plant and animal communities following human disturbance. Species abundance models based on plant traits and abiotic characteristics can also provide evidence of changes in ecosystem services (Lavorel *et al.* 2011).

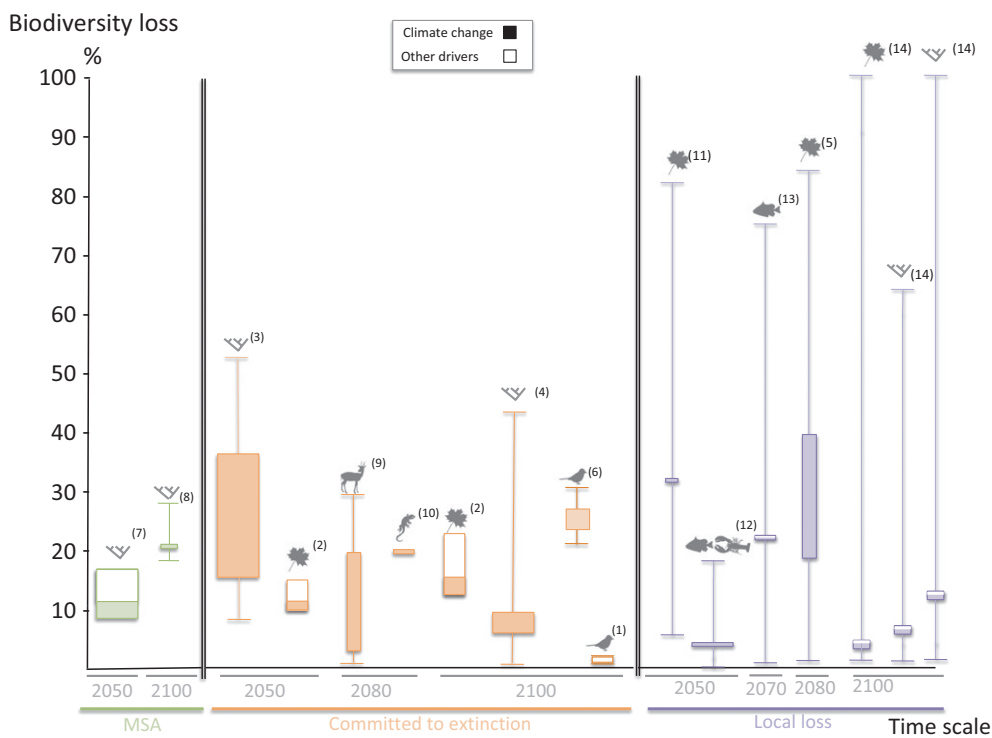
There are, however, several major limitations to these models, especially concerning the indices of biodiversity derived from DRR applied to species abundance. They depend largely on the quality of the input data (of which much more is needed than in most other models), uncertainty cannot be taken into account, and they are difficult to relate to commonly used biodiversity indices (Alkemade *et al.* 2009).

### Model combinations

Current modelling techniques usually incorporate a succession of one (or several) future socio-economic scenario(s), one (or several)



**Figure 3** Examples on successive combinations of socioeconomic scenarios, projections of extinction drivers, biodiversity range or species loss models and biodiversity metrics, leading to projections of biodiversity losses following climate change. Numbers correspond to references (see Appendix S2 for details and reference list).

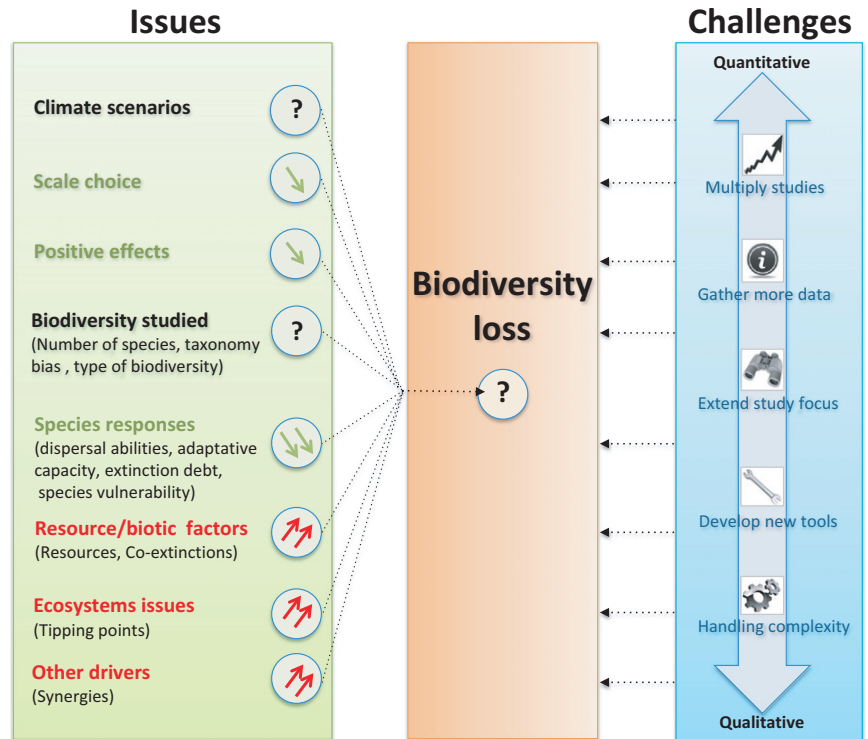


**Figure 4** Projections of loss of biodiversity due to climate change, for different taxonomic, temporal and spatial scales. The width of the box illustrates three levels of generality: global scale and several taxonomic groups (∞), global scale and only one taxonomic group, continental scale and only one taxonomic group. The box is delimited by the upper and lower boundaries of the intermediate scenario, while maximum and minimum values of the whiskers indicate the highest and lowest biodiversity losses across all projections. This figure illustrates that the different studies (i) generally predict significant biodiversity loss and (ii) use a combination of different biodiversity metrics, taxonomic groups and spatial scale and time horizon, making generalisations difficult. Numbers correspond to references (see Appendix S2 for details and references).

extinction driver(s), one biodiversity range or species loss models (Fig. 3). They then express their projections in terms of various extinction metrics. This has generated a variety of ‘model combinations’ leading to a wide range of projections that are not straightforward to compare, as the underlying assumptions differ greatly. We

have synthesised in Fig. 4 the results of all such projections made at a global scale either geographically or taxonomically. Despite important differences and some bias (e.g. marine biodiversity is still poorly represented), these models generally indicate that many species can be expected to decline rapidly at a global scale.

**Figure 5** Issues and challenges for climate change driven biodiversity loss. Examples of each are presented and discussed in the main text. The issues are in the first box, which represents the main factors of uncertainty and the direction of the likely current bias (green factors and arrow down is a likely overestimation, while red factors and arrow up is a likely underestimation; both can occur simultaneously, according to the approach taken in different studies; black factors and question marks are for unknown direction of misestimation; double arrow means very large expected effect). Challenge types range from quantitative (such as increasing the number of studies and the quantity of available data, or extend the focus of studies to include more factors) to more qualitative ones (developing new tools and progressing in resolving complexity).



### Projections of species loss

The field of climate change biology has thus followed several distinct and independent lines of model development (Fig. 3). This is potentially advantageous, as the convergent predictions can be regarded as an indication of robustness. In essence, the results show that local species extinctions cover an extremely large range, with some areas experiencing virtually no losses and others facing nearly complete loss of current species. High local losses can concern relatively large areas; for example, Bakkenes *et al.* (Bakkenes *et al.* 2002) estimated that more than 16% of European landmass would have local species losses exceeding 50% by 2050. This must be distinguished from projections of species extinctions at the global level, which are unsurprisingly lower than at the local level, since local extinctions do not necessarily lead to global extinctions. Nevertheless, even these global estimates suggest major losses of biodiversity due to global climate change that are generally higher than current rates of loss and far higher than rates of species extinctions documented in the fossil record (Pereira *et al.* 2010; Barnosky *et al.* 2011). For example, one of the earliest global studies estimated that by 2050 15–37% of species are committed to extinction under intermediate climate warming (Thomas *et al.* 2004). Birds are projected to be particularly sensitive to climate change. Two studies have calculated losses by 2100 due to climate change: these range from less than 0.3% of the world's 8750 species of land birds would be committed to extinction (Jetz *et al.* 2007) and up to 30% of the 8400 land bird species in the Western Hemisphere could go extinct (Sekercioglu *et al.* 2008). Regarding the vulnerability of 25 major biodiversity hotspots, Malcolm and colleagues suggested that the extinctions of endemic species could reach 39–43% under in worst-case scenarios, representing the potential loss of 56 000 endemic plant species and 3700 endemic vertebrate species (Malcolm *et al.* 2006).

Studies based on changes in species abundance generally predict an erosion of biodiversity in the same order of magnitude as species extinction models do, i.e. losses of 11–17% of MSA by the end of the century (Alkemade *et al.* 2009). Using data from 9856 birds, 6222 amphibians and 799 coral reefs, the IUCN forecasted that *c.* 35% of the world's birds, 52% of amphibians and 71% of warm water reef-building corals are particularly susceptible to climate change (Foden *et al.* 2008). Variability in local extinctions is significantly higher than in global extinctions projections. Indeed, in some regions the species composition will not change at all and in others almost all species will be lost following climate change. Estimated losses of riverine fish richness at a local scale vary considerably between 0 and 75% according to the river considered (Xenopoulos *et al.* 2005). Similarly, estimated local losses of plant diversity in Europe range from 2 to 84% of species lost per pixel (Thuiller *et al.* 2005).

Overall, the diversity of taxonomic groups studied, of biodiversity loss metrics, of spatial scales and time periods render complex and uncertain comparisons between these studies. In addition, the large array of modelling techniques further complicates the comparisons. Moreover, several studies assess the combined effects on future biodiversity of both climate change and land use, making it difficult to distinguish the effect of each. Finally, there is growing concern that the underlying assumptions of all of these models could lead to large over- or underestimations of potential species losses (Pereira *et al.* 2010; Dawson *et al.* 2011). These are summarised in Fig. 5. As an example, a recent study suggests that the realised effects of climate change might far exceed the current predictions (Maclean & Wilson 2011). Based on a global multi-taxa meta-analysis of recorded ecological responses, they estimated that the mean observed extinction risk by 2100 is systematically higher than the mean predicted extinction risk across the theoretical studies considered in the meta-analysis: 12.6% in plants (vs. 4% predicted), 9.4% in inverte-

brates (vs. 7.2% predicted) and 17.7% in vertebrates (vs. 12.4% predicted). Overall, these estimates of biodiversity loss are obviously a major concern.

### WHAT FURTHER IMPROVEMENTS ARE NEEDED?

Climate change ecology is still in its infancy, and tremendous improvements are made rapidly in virtually all aspects of this emerging field. Critical requirements to be able to predict future trends include the need to study a much larger part of biodiversity, to overcome several major model limitations, to account for co-extinctions and other major drivers of biodiversity loss and to validate models by comparing projections with observations. These limitations are detailed below. Figure 5 provides a summary of the directions in which each of these weaknesses is likely to affect the current projections on biodiversity loss, as well as the major types of challenges that have to be faced to overcome these uncertainties.

#### Climate scenarios

Climate scenarios depend on a wide range of socio-economic storylines for greenhouse gas emissions in the future, including the Special Report on Emissions Scenarios Millennium Assessment and Global Biodiversity Outlook scenarios (Pereira *et al.* 2010), and on a broad suite of General Circulation Models used to calculate climate change for given trajectories of greenhouse gas emissions. This means that the projections of species loss can yield highly contrasting results depending on the choice of combinations of emissions scenarios and climate models, independently of the model of biodiversity response that is used (Beaumont *et al.* 2008). In addition, internal climate model variability could result in greater differences in projected species' distributions than variability between climate models (Beaumont *et al.* 2007). In addition, 4–39% of the world's landmass will experience combinations of climate variables that do not currently have equivalent values anywhere on the globe (so called no-analogue climates, Williams *et al.* 2007). One key challenge is to provide robust and credible uncertainty intervals for all model outcomes and, if possible, to reduce them.

#### Scale choice

The choice of the spatial resolution scale is probably one of the most important factors generating variability. For example, a coarse, European-scale model (with 10' × 10' grid cells) predicted a loss of all suitable habitats during the 21<sup>st</sup> century, whereas a model using local-scale data (25 × 25 m grid cells) predicted persistence of suitable habitats in up to 100% of plant species (Randin *et al.* 2009). These differences are probably explained by the failure of coarser spatial scale models to capture both local topographic diversity and habitat heterogeneity (Luoto & Heikkinen 2008; Randin *et al.* 2009). On one hand, global models can be used for a large number of species but focus on one type of species' response and therefore lack biological realism. On the other hand, population or species models provide insight into a very limited range of species, typically at regional scales (i.e. adaptation phenology, dynamic population) but cannot provide global scale trends. This is a classical trade-off between precise small-scale models and coarse large-scale models that lack biological realism (Thuiller 2003).

### Positive effects

Climatic changes could also have positive effects on biodiversity. For instance, more clement temperatures and increased CO<sub>2</sub> are likely to be beneficial to many plants, resulting in an acceleration of biomass production. Milder winters might increase survival of many currently threatened species in temperate regions. Increased precipitation may also benefit some plant communities and species depending on them. Moreover, several studies reported detrimental effects of climate change on biological invasions (e.g. Peterson *et al.* 2008). Although few studies report beneficial effects of global changes on biodiversity, they certainly exist and add to the difficulty of getting a clear overview of the effects of climate changes on the biodiversity of our planet.

### Biodiversity measures

Even in the most ambitious studies, the range of species studied always represents a small percentage of known biodiversity. All studies are taxonomically biased, as they generally concentrate on a few conspicuous taxonomic groups such as plants, mammals and birds (Thuiller *et al.* 2011), with a particularly strong bias towards terrestrial vs. marine biodiversity. However, it is generally recognised that the vast majority of biodiversity in terms of species richness, evolutionary divergence, biomass and even ecosystem functioning is represented by 'cryptic biodiversity', especially micro-organisms and insects (Esteban & Finlay 2010). Similarly, there are important biases in data collection both across regions and ecosystems (McMahon *et al.* 2011). Furthermore, most studies focus on species richness, because it is thought to influence the resilience and resistance of ecosystems to environmental change. However, a few studies have explored the impact of climate change on functional (Thuiller *et al.* 2006) and phylogenetic diversity (Thuiller *et al.* 2011), and the effects on genetic diversity are only beginning to be explored. Moreover, it is likely that different levels of diversity are affected differently by climate change, so these should be evaluated in parallel to provide a broad picture of biodiversity response to climate change (Devictor *et al.* 2010).

In addition, there are different indicators of biodiversity change, such as the number of species 'committed' to extinction (Thomas *et al.* 2004; Pereira *et al.* 2010), extinction risk (Thuiller *et al.* 2005), or change in abundances (Alkemade *et al.* 2009; Leadley *et al.* 2010). The number of species 'committed' to extinction is probably not the most appropriate metric to forecast the future of biodiversity because the extinction debt could vary from decades to centuries (Kuussaari *et al.* 2009). A complementary metric of biodiversity can be changes in MSA, which is an index defined as the mean abundance of original species relative to their abundance in undisturbed ecosystems. As extinction is only the last step in the process of species decline, the MSA can provide a metric to evaluate ecosystem degradation. In addition, we need new approaches to predict the impacts of climate change at the community level (i.e. Mokany & Ferrier 2011). Currently, neither the estimates of species losses nor of the qualitative impacts on ecosystem functioning and services are satisfactory to give a global overview of the impacts of climate change (Dale *et al.* 2010).

### Limitations of predictive tools

Each of the modelling approaches reviewed has methodological, spatial and temporal limitations that constrain their predictive power

(e.g. McMahon *et al.* 2011). In general, models do not take into account the multiple responses of species to climate change, but rather focus mainly on one axis, spatial shifts of potential habitat (Fig. 2). The temporal and the physiological responses are generally overlooked, as are the genetic and plastic capacity of species (Lavergne *et al.* 2010; Salamin *et al.* 2010). In addition, species are commonly considered as static and independent entities, although their dynamics and their role in ecological networks are both known to be essential. However, a new generation of models is emerging that focuses on more realistic biological hypotheses and meets some of the challenges posed by each limitation (e.g. Thuiller *et al.* 2008; Brook *et al.* 2009; Gallien *et al.* 2010).

### Species responses

Current global extinction models make very coarse assumptions about species responses. For example, the dispersal capability is a major issue for projections of future biodiversity. Until recently, models often addressed dispersal issues by using two extreme assumptions of either unlimited or no species dispersal (Thomas *et al.* 2004). This is clearly convenient for practical purposes, but most species are between these extremes. In addition, exceptional occurrences of long-distance dispersal are thought to have helped past species surmount prehistoric climate changes (Dawson *et al.* 2011 and references therein). Although rare, these events are of crucial significance in the current context, as they could in many cases make the difference between species survival and extinction, especially as human-mediated long-distance dispersion is now common for many organisms.

Inherent differences in vulnerability are not always taken into account when making large-scale correlative predictions of the future of biodiversity. Indeed, most models work under the very strong hypotheses that species currently live in an optimal climatic niche and that they cannot survive if there is a change in the climatic conditions that contribute to define this niche. Such a hypothesis amounts to overlook the potential of adaptability of species. Numerous studies have shown that species are capable of fast responses through phenotypic plasticity or microevolution (Lavergne *et al.* 2010). Before being able to forecast species trajectories with some credibility, we therefore need to assess properly the vulnerability of species (including exposure, sensitivity, adaptive capacity and migration potential), habitats and regions to different components of climate change (Dawson *et al.* 2011; McMahon *et al.* 2011). Despite growing evidence for rapid adaptive evolution in response to climate change, the consequences of such evolution on species persistence remain to be explored (Lavergne *et al.* 2010). Currently, more flexible models of micro-evolutionary processes combine population-based information with phylogenetic comparative methods to provide an estimation of the evolutionary potential (Salamin *et al.* 2010). Moreover, populations can be locally adapted to specific climatic conditions and therefore, models treating a species as a single homogeneous unit might be flawed. Consequently, studying under which circumstances losses in genetic and species diversity at local to regional scales occurred in the past could improve models outputs (Dawson *et al.* 2011; McMahon *et al.* 2011).

### Population and metapopulation dynamics

An inherent property of current global extinction models is that they do not take into account population or metapopulation dynamics that

determine species distributions, population structure and extinction risk at a local scale. Models are often based on habitat reduction and do not offer a mechanism by which the species' fitness is reduced and ultimately led to extinction. Recently, new mechanistic niche models have endeavoured to estimate key fitness components such as survival, growth, development and reproduction as a function of species attributes (i.e. physiology, phenology, behaviour) that vary with climatic conditions (Kearney *et al.* 2010).

Currently the probability of extinction is based on a projection of suitable habitats entirely lost (species will be committed to extinction) or partially lost (species will increase their extinction risk), although it is possible to combine niche models and abundance data (Iverson & Prasad 1998). In fact, on one side some species are more likely to go extinct because they consist of small and disconnected populations and on the other side, some species have shown compensatory changes in demographic rates following climate change (Doak & Morris 2010). The approach of population viability analysis (PVA) in this context could provide a good alternative. It is used to estimate the likelihood of a population's extinction within a given number of years through the species' demographic characteristics and environmental variability, instead of species range shifts. Only a few studies have used PVA to predict the effects of climate change on extinction risks (Keith *et al.* 2008; Anderson *et al.* 2009), in part because this approach requires data on population dynamics that are not available for most species.

In addition, physio-demo genetic models could provide the most realistic method to forecast the future of key species, as they consider simultaneously demographic (e.g. growth, rate of survival and reproduction, migration processes, environmental stochasticity), physiological (e.g. metabolic rate) and genetics parameters (heritability and norm of reaction). However, studies using physio-demo genetic models to evaluate the impacts of climate changes remain scarce (Kramer *et al.* 2010).

### Co-extinctions

Whether centred on a single species or taking into account large taxonomic groups, most studies and all models have disregarded interspecific relationships such as competition, facilitation or mutualism. Beyond single-species extinctions, both direct and indirect processes can lead to cascading and catastrophic co-extinctions, also called 'chains of extinction' (Brook *et al.* 2008). Despite the importance of interspecific interactions, these relationships are exceptionally difficult to model; this is especially cogent in the context of lack of data on population dynamics and trophic webs (McMahon *et al.* 2011). As each species comes with its cortege of specific parasites and symbionts, as well as many trophic relationships, the consequences of global change on biodiversity might be substantially underestimated when focusing on species-specific extinction rates (Koh *et al.* 2004; Yang & Rudolf 2010). There is an urgent need not only to go beyond the single-species approach, but also to get past the species richness approach and to consider interspecific interactions, trophic webs and ecological networks (Bascompte 2009).

### Synergies between extrinsic drivers of extinction

Research on future species extinctions has so far mostly considered a limited set of the predicted changes. For example, sea level rise has seldom been considered, although the most recent scenarios

projecting up to 2 m of rise by 2100 are raising new concerns for coastal and insular biodiversity (Grinstead *et al.* 2009). In addition, studies have mainly focused on the sole impact of climate change, sometimes considering a single additional driver (e.g. land-use change). These limitations may often lead to overly optimistic estimates. Indeed, other components of global change, such as habitat fragmentation, pollution, overexploitation and biological invasions have all been documented as major, additional threats for the future of biodiversity, with possible synergies, or reinforcing feedbacks between them (Sala *et al.* 2000). For instance climate-induced facilitation of invasions can occur at all stages of the invasion process (Walther *et al.* 2009; Bradley *et al.* 2010). In an experimental context, habitat fragmentation and overfishing combined with global warming have led to a decline in rotifer populations of up to 50 times faster than when either threat acts alone (Mora *et al.* 2007). In this case, dose-response relationship models could offer a powerful approach because they could simulate the impacts of many drivers of species extinctions.

Overall, despite important uncertainties and much conflicting imprecision, both under- and overestimating species loss, the very large underestimations due to co-extinctions, synergies and tipping points are extremely worrisome for the future of biodiversity (Fig. 5). Given the attractiveness of quantitative projections from mathematical models, it is tempting to underestimate their limitations. To minimise this risk, it is crucial to use a variety of complementary approaches, ranging from observational studies (palaeontological data, phenological responses, adaptive capacity) to field and laboratory experiments (on genetic, species and ecosystem levels) (Dawson *et al.* 2011).

## BIODIVERSITY MANAGEMENT

The large variation of responses of different species necessitates the use and integration of multiple approaches to further our understanding of the impacts climate change can have on biodiversity (Dawson *et al.* 2011). Similarly, our responses in terms of biodiversity management ought to transcend disciplines. Beyond this, global climate change prompts several methodological issues and the implications for conservation and management of biodiversity and ecosystem services.

### Conservation of species and ecosystems

The large projected impacts of climate change on biodiversity at all levels mean that ecologists must quickly rise to the challenge of providing scientific guidance for the development of conservation strategies (Pressey *et al.* 2007; Araújo *et al.* 2011; Dawson *et al.* 2011). A major role of conservation planning is to design reserve networks that protect biodiversity *in situ*. Currently few studies have attempted to use modelling for conservation purposes (Araújo *et al.* 2011). It is increasingly important to protect the heterogeneity of habitats as well as genetic diversity within a species to sustain the capacity of a species to adapt. Also, the characteristics of protected areas, where planning has to be done decades in advance (Hansen *et al.* 2010), need to be reviewed under climate change. Climate modelling can help to re-evaluate the current set of protected areas, their places, size, layout and design (Araújo *et al.* 2011). In particular, protection should be prioritised for places that minimise the effects of climate change – like forests, which contribute strongly to local climatic conditions – as well as for climate refuges for biodiversity (Carnaval *et al.* 2009).

Finally, model predictions of where, when and how future risks may affect species, biomes or ecosystems could assist in identifying the most appropriate conservation measures. For instance, species or ecosystem projected to be primarily affected by climate change may require adapted measures compared to species negatively affected by land-use change that could persist through protection of their remaining natural habitat (Hannah *et al.* 2007). In many cases there may no longer be any overlap between a species' current range and its possible future range. As this situation will lead to extinction, climate change has been a major argument for the proponents of human-assisted colonisation (Loss *et al.* 2011). In this increasingly hot debate, case-by-case decisions have been advocated, based on the balance between threatened status of a species and threat of that species for the recipient ecosystem, as well as the socioeconomic context in which conservation is taking place (Richardson *et al.* 2009; Dawson *et al.* 2011). A widespread view is that an important strategy is to enhance landscape connectivity to enable species to move through a matrix of interconnected habitats to favour escapes from unsuitable climatic conditions (Hannah *et al.* 2007).

It is also essential to shift from a species centred focus to a holistic view encompassing species interaction networks, and other aspects of biodiversity such as functional and phylogenetic diversities (Devictor *et al.* 2010). Beyond these various strategies, there is a growing call to go past the predictive focus and start aiming for an integrated and unified framework to identify species vulnerability and adapt biodiversity management interventions (Dawson *et al.* 2011). In this regard, preventive actions are of foremost importance. For example, it should be remembered that the proportion of species extinction is a power function of the expected global warming (Hansen *et al.* 2010). Minimising global warming could therefore have nonlinear effects in the preservation of species from extinction, with each tenth of degree avoided saving an increasing number of species (Hansen *et al.* 2010). Acting to reduce global warming itself, and not only its effect on biodiversity, should remain *a priority* in conservation sciences. In addition, reducing other global change drivers could increase overall resilience of biodiversity in the face of climate change (Hughes *et al.* 2003).

### Ecosystem services

Other aspects of biodiversity management will be affected by global change and will need adapting, including wildlife exploitation [e.g. forestry (Dale *et al.* 2010) or fisheries (Stram & Evans 2009)], agronomy (Howden *et al.* 2007), pest and invasive species control (Ziska *et al.* 2011) or human and wildlife disease management (Harvell *et al.* 2002). For example, major challenges in agronomy include the need to shift to species or varieties better adapted to particular components of climate change or to rethink strategies to control invasive and pest outbreaks, finding solutions in the increasing competition for water between the natural and the agricultural ecosystems, improving infrastructures and adapting cropping systems to meet future demands of a growing population living on poorer biodiversity resources (Howden *et al.* 2007).

Given the tremendous ecological impact of alien invasive species, and the expected exacerbation of invasion due to climate change (Walther *et al.* 2009), it is urgent to increase predictive power in this field. It is also crucial to move beyond predictions (Dawson *et al.* 2011) and to strengthen risk assessment, protocols of screening and of early detection, vector control and integrated management in area

and/or of invasive species that will become at higher risk following climate change. Similar efforts are imperative for other drivers of biodiversity loss, such as overexploitation or habitat destruction.

## CONCLUSION

Ecologists are developing a better understanding of the mechanisms by which species and ecosystems can be impacted by climate change. The timing of species' life cycle events is expected to be further altered, species distributions will change radically, trophic networks will be affected and ecosystem functioning may be severely impaired, leading in the worst cases to countless species extinctions. Over the past decades, some of this understanding has been effectively translated into mathematical models that can be used to forecast climate change impacts on species distributions, abundance and extinctions. These models are characterised by their high diversity of underlying structures and assumptions, with predictions differing greatly depending on the models used and species studied. Most of these models indicate alarming consequences for biodiversity with worst-case scenarios leading to extinction rates that would qualify as the sixth mass extinction in the history of the earth (Barnosky *et al.* 2011). However, all current approaches have serious weaknesses. An evaluation of known mechanisms of climate impacts on biodiversity suggests that the lack of several key mechanisms in models may lead to either very large underestimations or overestimations of risks for biodiversity. Improvements in existing models and, in particular, a new generation of models must address the shortcomings of current models to reduce uncertainties. It is also crucial to improve our understanding of the vulnerability of biodiversity to climate change, to develop other predictive approaches and to go beyond predictions.

Crucially, the diversity of approaches, methods, scales and underlying hypotheses used has led to an ensemble of global quantitative predictions that can seldom be compared. Consequently, we are left with a mosaic of information that cannot provide a quantitative, coherent picture of future biodiversity loss. Yet, standardisation of future studies (of taxonomic groups, methods, time horizon, scale, etc...), which might help decrease uncertainty, would do so at the expense of the breadth of knowledge and of a much needed innovation in this field. In this regard, a solution may come from a collective effort in conducting large meta-studies that would encompass many components of variability (biodiversity, time and space scale, models,) to both infer similarities and assess sources of inconsistency. Given its scale, such an ambitious endeavour needs an enduring cooperative effort from coordinated research groups. The long awaited Intergovernmental Platform on Biodiversity and Ecosystem Services (Perrings *et al.* 2011) could provide the impetus for building such national and international efforts. A major near-term target to substantially improve our understanding, predictive capacity and reactive potential will be to contribute to this new IPCC-like assessment for biodiversity and ecosystem services.

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## Biological invasions – a major threat to biodiversity





# A short introduction to biological invasions



# 3. BIOLOGICAL INVASIONS

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## 3.1. A short introduction to biological invasions

All components of global change tend to increase. In addition, invasion of species into new territories (biological invasion) is classically listed as the second most important threat<sup>1,2</sup>. The Invasive Specialist Group of the International Union for Conservation of Nature, (IUCN) describes invasive species as “animals, plants or other organisms introduced by man into places out of their natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species. Invasive species can negatively impact human health, the economy (i.e. tourism, agriculture), and native ecosystems. These impacts may disrupt the ecosystem processes, introduce diseases to humans or flora and fauna, and reduce biodiversity”<sup>3</sup>. The exact definition of invasive species has been disputed, for example Valéry et al.<sup>4,5</sup> (but see<sup>6</sup>) dispute the reservation of the term ‘invasive species’ to allochthonous species and advocate to extent the definition to native (non-introduced) species because native species can, under some circumstances, also undergo demographic explosions as a result of modifications of the environmental conditions. Some also propose not to put the emphasis on the impacts of invasive species because these are difficult to quantify<sup>7</sup>. Moreover, the notion of ‘invasive species’ as such has been questioned by Davis et al.<sup>8</sup> who believe that the distinction between natives and invasives is based on an anthropocentric, xenophobic point of view. They argue that most observed impacts are limited to particular ecosystems (e.g. islands) and a small number of species and that many invasive species can actually have a positive impact<sup>8</sup>. However, this view is not shared by the majority of invasion biologists who have accumulated a large body of literature on the ecological impacts of invasive species<sup>9</sup>. It has been argued that many criticism of invasion biology as a science are largely due to misunderstandings and misuse of the terminology<sup>10</sup>. In fact, nobody disagrees that only a small proportion of introduced species will eventually have a negative impact on biodiversity and only when such an exotic species becomes problematic it is defined as “invasive”. According to the Tens Rule only about 10 % of introduced species establish themselves in the new environment and about 10% of these, in turn, become harmful “invasives”<sup>11</sup>. But this percentage depends on the taxonomic group and the invaded environment and can be much higher<sup>12</sup>. For example, among aquatic species introduced to several European countries, 69% of established populations had ecological impacts<sup>13</sup>.

Another challenge for the definition of invasive species are on-going global changes. For example, as the climate changes many species will move in space in order to track their climatic niche<sup>14-16</sup>. If those species have an impact on native species, they may be considered as invasive under some definitions<sup>17</sup>. However, if human-mediated transport is part of the definition, they should not be considered as invasive.

In the context of this thesis, I will focus on species that are already considered as invasive by the ISSG and I will adopt their definition of invasive species that includes three main elements: 1/ introduction of the species outside of its native range, 2/ demographic explosion and 3/ negative impacts.



### Invasive species

There are 891 species listed as 'invasive' by the ISSG <sup>3</sup>. These species come from very diverse taxonomic groups ranging from mammals, birds, plants to invertebrates and microorganisms. A recent study has found that the number of documented invasive species per country ranged from 9 in Equatorial Guinea to 222 in New Zealand, demonstrating that invasive species are a global problem <sup>18</sup>. The majority of countries fell in the lowest class of invasive species richness (Fig. 1) but the highest proportion of these countries were considered data deficient. Therefore, the number of invasive species is likely to be underestimated <sup>18</sup>.

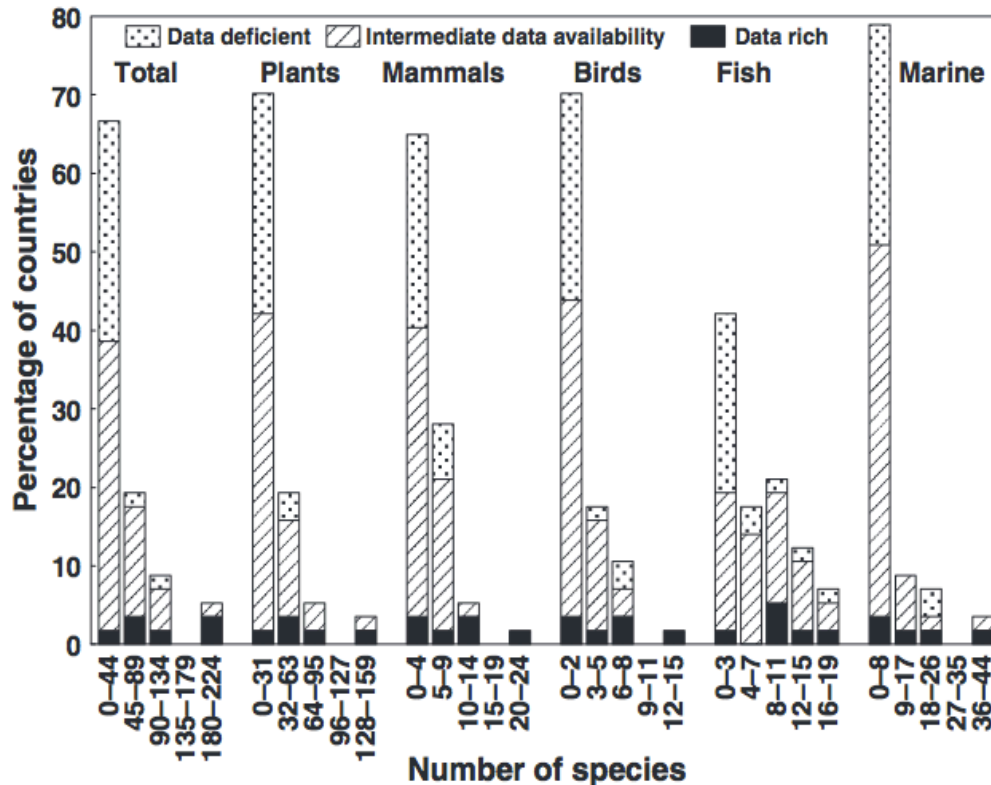


Fig. 1 Reproduced from McGeoch et al. <sup>18</sup>: Frequency distribution of the number of Invasive alien species (IAS) across 57 countries with different degrees of data adequacy (18 data deficient, 33 intermediate, 6 data rich countries).

### Introduction pathways

Biological invasions are becoming more frequent due to the increased rate of human-mediated transport of exotic species as a result of commercial and touristic exchanges between countries <sup>19</sup>. Humans introduce species for a variety of different reasons. Some are simply introduced by accident with cargo or ship ballast <sup>20</sup> (Fig. 2). This is especially relevant for small sized individuals such as insects, plant spores or small marine invertebrates that are easy to transport in this way. Other species, however, are introduced deliberately as agricultural crops, livestock, pets or even as biological control agents (Fig. 2).

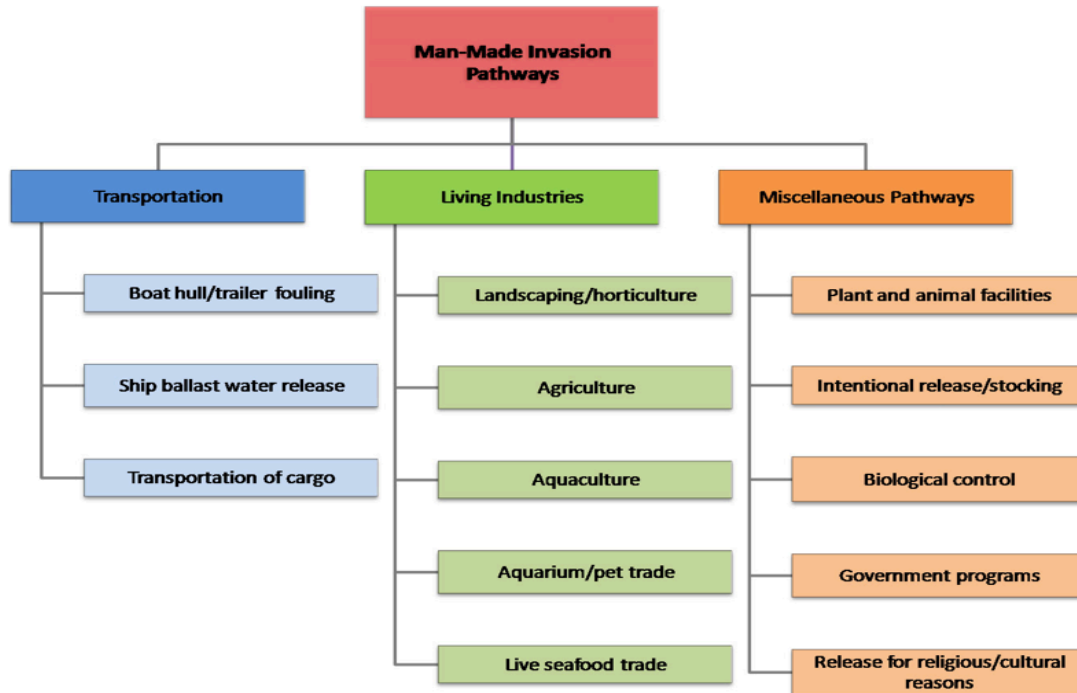


Fig 2 Invasive pathways <sup>20</sup>

A recent study <sup>19</sup> has shown that the number of introductions across many different taxonomic groups, including plants, fungi, birds, mammals, amphibians and reptiles, fish, insects and aquatic invertebrates, has steeply risen over the last century (Fig. 3). They demonstrated that across all taxonomic groups analysed, indicators of historic introduction efforts around the year 1900 explain current numbers of invasive species in Europe significantly better than the same indicators evaluated for the recent past <sup>19</sup>. Given the enormous increase in human-mediated species introductions during the second half of the 20<sup>th</sup> century, this result implies an important delay between the introduction of a species and its subsequent establishment <sup>19</sup>. The authors suggest that this delay “probably results from the time necessary to exceed critical thresholds of available propagules that will, in turn, depend on factors like the numbers of introduction events and of individuals introduced, the type of introduction pathway, the match between an alien-species’ habitat requirements and the conditions in the new territory, the length of generation times, or the time necessary for genetic adaptations to the new environments.” <sup>19</sup> This time lag between the introductions and the actual invasions implies that we do not yet witness the numerous invasions that we are causing today due to increased socioeconomic activities.

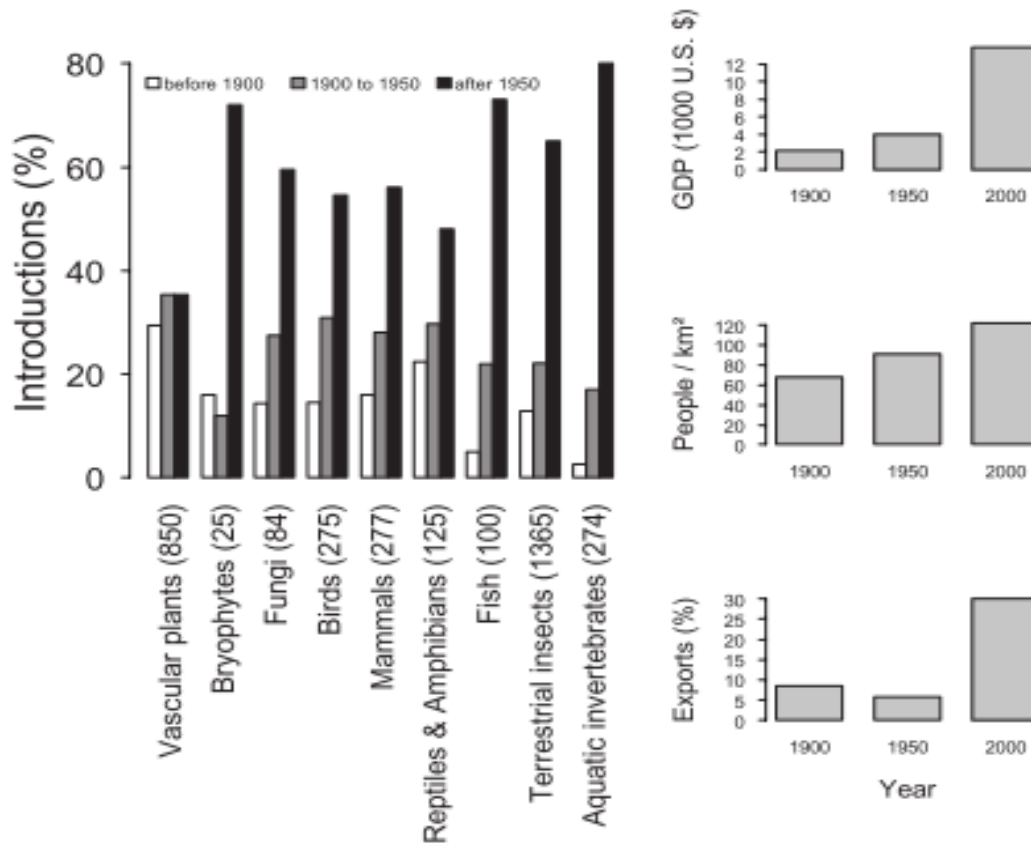


Fig. 3 From Essl et al. <sup>19</sup>: “Left: Percentages of introduction events for different taxa recorded in the European countries before 1900, between 1900 and 1950, and after 1950. Numbers in parentheses represent the overall number of species per taxon with known introduction dates. Right: Average trends in three socioeconomic indicators: per capita GDP, population density, and the share of exports in GDP at three different time points (1900, 1950, 2000) for the 28 European countries used in this study”.

### Impacts

Invasive species can affect native species in a variety of ways. Invasive species can be predators (cats), pathogens (North American chestnut blight causing the Irish potato famine; Ebola virus devastating gorilla populations, West Nile virus infecting many bird populations), herbivores (rabbits in Australia, deer in New Zealand) and competitors (American mink displacing European mink, Argentine ants displacing native ants) <sup>21</sup>. The decline of the population of a native species can ultimately lead to the local displacement of the species and even global extinction. Biological invasions are responsible for many species' extinctions over the world, as exemplified by introduced rats and cats on islands <sup>22</sup>. In fact, biological invasions have been a key factor in 54% of known animal extinctions and the only factor in 20% of extinctions <sup>23</sup>. A recent study has analysed the drivers of changes in the Red List Index for different taxonomic groups and shown that the impact of invasive species on the species status has increased relative to other threats <sup>18</sup>(Fig. 4). Most extinction events have so far happened on islands, which have a high level of endemism and where native species have often evolved in the absence of strong competition, herbivory, parasitism or predation <sup>24</sup>. For example, many islands have a number of ground-nesting bird species that are not at all adapted to predation by cats or rats.

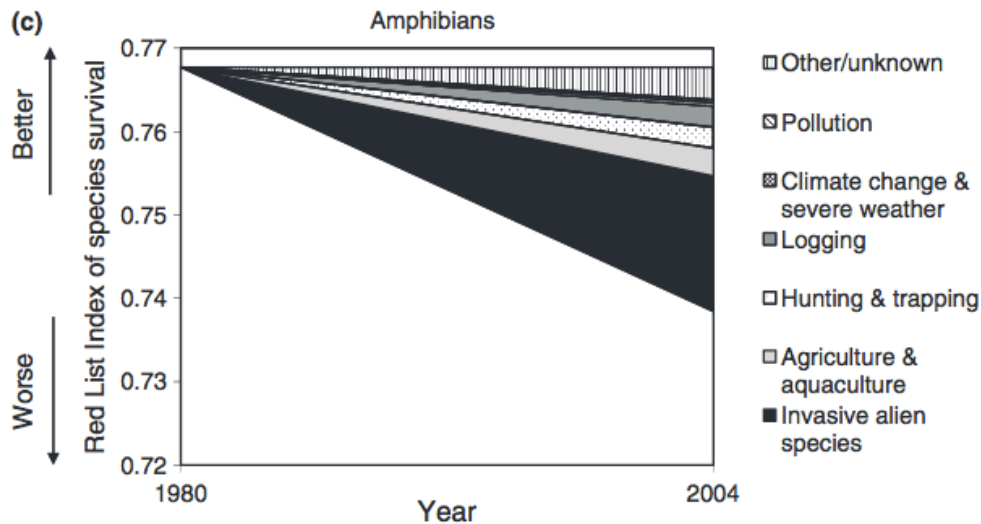


Fig. 4. From Mc Geoch: Red List Index for amphibians showing trends driven by the impacts of invasive alien species compared with trends driven by other factors.

Furthermore, the introduction of non-native species causes important modifications in native communities and thereby in ecosystem functioning, sometimes severely impairing ecosystem services<sup>21</sup>. In addition to major ecological damage worldwide, biological invasions impose a tremendous cost on society. A recent assessment of their impacts in Europe reported that control, research, prevention and monitoring programmes for invasive species as well as damages to infrastructure, agriculture, fishing, forestry and human health cost Europe a total of over 12.5 billion euros per year<sup>25</sup>. Pimentel et al. estimate that the United States incurs a total of 120 billion US \$ annually in damages associated with invasive species – with one species of ant, the red imported fire ant, being responsible for the loss of 1 billion US \$<sup>26</sup>. It has been suggested that the range and impacts of invasive species could even further increase with global climate change.

#### Management & Eradication

Management and control options of invasive species are available but are often associated with high economic costs and practical difficulties, both of which increase rapidly the longer an invasive population has been established<sup>27</sup>. Therefore, the best strategy is to manage the population as early as possible. In total, 82% of eligible countries have signed international agreements relevant to preventing the spread and promoting the control/eradication of IAS. Successful eradications/control of IAS include pigs on Clipperton Atoll, France, cats, goats and sheep on Natividad, Mexico, and red fox in southwest Australia<sup>28</sup>. Yet, management of invasive species is complex and requires the interplay of numerous scientific and political agents as well as the general public (Fig. 5).

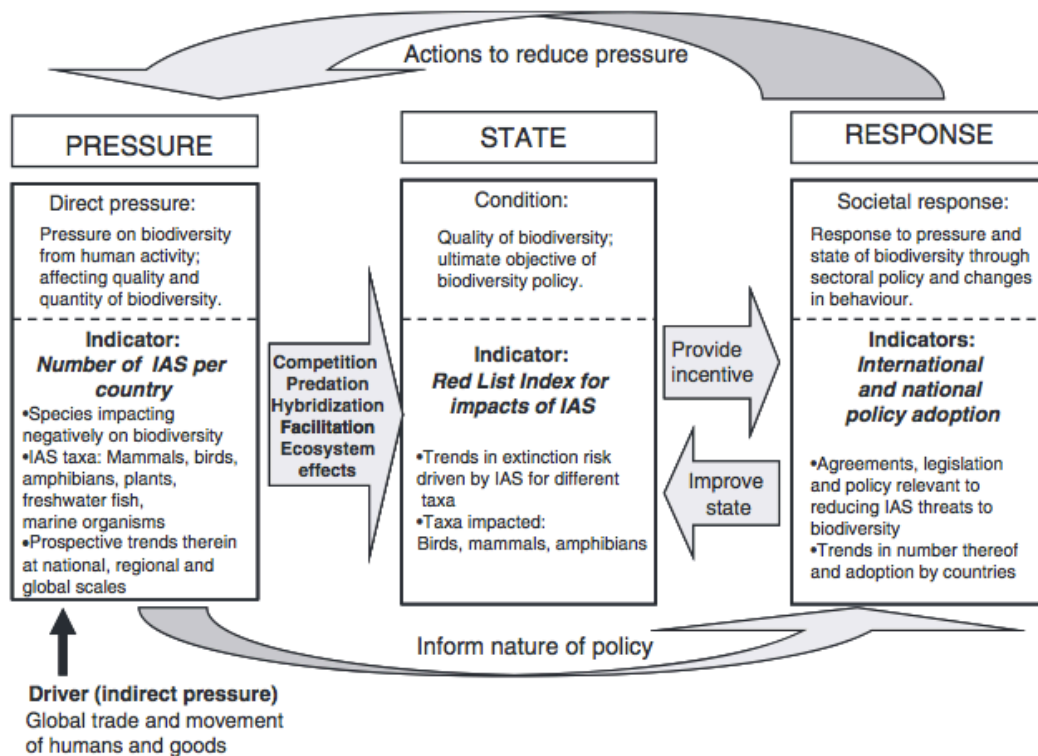


Fig. 5 From Mc Geoch et al.<sup>18</sup>

Large difficulties can stem from communication problems with the general public who does not support eradication campaigns. This can be the case if the invasive species is especially 'cute' such as the Siberian Chipmunk that has been sold in European pet shops and released by owners into the wild or plants<sup>29</sup> or animals that can have strong cultural or agronomic values. Consequently, there is a need to communicate about invasive species and to clarify the distinction between native, exotic and invasive species. It has to be underlined that the terminology attached to 'invasion biology' is not an expression of xenophobic ideas<sup>21</sup>, but that invasive species can have an actual devastating impact on biodiversity, agriculture, health and economy<sup>9</sup>. One tool to communicate about invasive species is the "100 of the worst invasive species" list that the ISSG set up to popularize the concept of invasive species and to raise the general awareness of the issue<sup>30</sup>. The following part is about the selection of a new 100<sup>th</sup> invasive species, led by our group, following the eradication of the rinderpest virus.

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## The 100th of the world's worst invasive alien species

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## The 100th of the world's worst invasive alien species

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**Abstract** Biological invasions are among the greatest threats to global biodiversity, but in contrast to most other global threats, they suffer from specific communication issues. Our paper presents the first new addition to the widely cited IUCN list of “100 of the world’s worst invasive species”, a list created a decade ago in response to these communication issues. We briefly present this list, the recent removal of one species from that list, and the rationale to include a novel, 100th species to replace it. The new species of this list, giant salvinia (*Salvinia molesta*), was chosen by the community of invasion biologists (over 650 experts from over 60 countries). This new addition to the list will draw public attention to the damage caused by invasive alien species and it will help stimulate the necessary discussion of this critical issue in science and policy circles.

**Keywords** *Salvinia molesta* · Biological invasions · ISSG

### Introduction

Although invasive alien species (IAS) are regarded as the second largest threat to biodiversity worldwide (after habitat loss; Clavero and Garcia-Berthou 2005; Simberloff et al. 2013), and their economic cost probably exceeds US\$300 billion per year worldwide (Pimentel et al. 2000; Genovesi 2011), the increased adoption of specific legislation by many nations has had limited effect on the rate of new introductions (McGeoch et al. 2010). In Europe for example, over twelve thousand alien species have been documented (Hulme et al. 2009), with an increase of over 76 % in alien species over the last 40 years (Butchart et al. 2010). Despite the progress of a large, dedicated community of researchers and managers worldwide, management successes against invasive alien species are still outnumbered by new introductions. Obviously, our improved knowledge about the harm they can cause, better management procedures to prevent new introductions, and more efficient eradication protocols remain insufficient (Genovesi 2011). New introductions in fact parallel the increase in intercontinental transportation of goods and people, which allows species to overcome long distances and geographical barriers. In addition, owing to the frequent time lags between introduction and observed impact,

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the full extent of current invasions will not be recognized for several decades (Essl et al. 2011). Biological invasions might also increase further in the future because of global environmental changes, in particular climate and land use changes (Walther et al. 2009; Bellard et al. 2013).

### Need to communicate about IAS

Although the current biodiversity crisis has generated concern both among the general public and with decision makers, IAS have proven difficult to deal with. In particular, awareness of the threat represented by biological invasions is impeded by the lack of a clear, identifiable target, owing to the tremendously high number of IAS and the even higher number of species that have the potential to become invasive. Consequently, not only are the programs aiming to limit the impacts of IAS still insufficient, but also the very awareness of the threats caused by IAS remains diffuse. Given these difficulties, invasion biologists have recognized that the need to communicate more efficiently and authoritatively is a key to success. Yet, among so many species of microorganisms, plants, invertebrates, and vertebrates, marine, freshwater, and terrestrial alike, communication efforts are often diluted, whereas specific targets are better at eliciting attention from the public and decision makers. In 1999, the International Union for the Conservation of Nature (IUCN), through its Invasive Species Specialist Group (ISSG) of the Species Survival Commission, set up a remarkable communication tool to address this issue: a list of 100 high-profile invasive species, all known to be tremendously harmful and prompting a dire need for conservation action. Subsequently, the list of “100 of the world’s worst invasive alien species” has boosted global awareness.

### 100 of the world’s worst invasive species

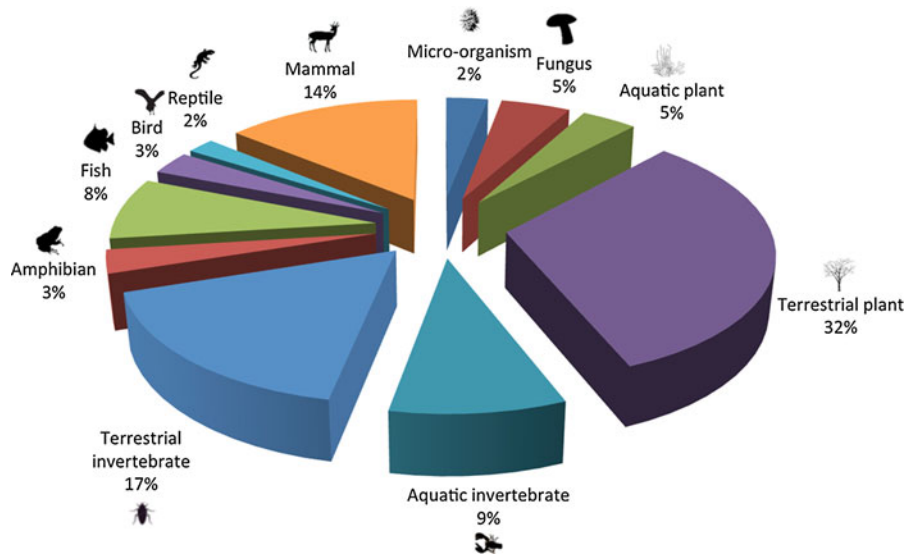
This list of 100 species was derived according to two criteria: their serious impact on biodiversity and/or on human activities, and their potential to illustrate important issues surrounding biological invasions (Lowe et al. 2004). To ensure the inclusion of a wide variety of examples, only one species from each genus was selected. As a result, the 100 species belong to

many taxonomic groups, from microorganisms to plants and vertebrates (Fig. 1). They come from all continents and have impacts on local biodiversity and ecosystem functioning, and on agriculture, forestry, or aquaculture; they affect landscape or real estate values and constitute health hazards, as allergens or as disease vectors. Two points were relentlessly emphasized as this list was promoted. First, absence from the list does not imply that a species poses a lesser threat. Second, these are not the 100 worst invaders, but 100 among the worst. Evidently, it would be very hard to rank diverse species with such varied impacts. The aim of this list was to highlight the importance of invasive alien species, by emphasizing those that belong to the list, but avoiding at all cost downplaying the importance of the thousands of species not on this list.

This list has been a tremendous success in terms of communication, with over 1,000 citations in the scientific literature and a number of similar lists promulgated for different regions or environments (e.g., Strefataris and Zenetos 2006; Vilà et al. 2009). Among the achievements is the successful global eradication of the rinderpest virus, a mere decade after the list was constructed, which reduced it to 99 species (World Organisation for Animal Health 2011). Subsequently, it was decided to replace the eliminated species, to keep the list at 100, rather than working to reduce it progressively. This course of action has the double advantage of highlighting yet another major invader and insisting on the fact that species that are not on the IUCN 100 list can nonetheless be among the worst invaders worldwide. On the contrary, constantly reducing the list would have given the misleading impression that IAS were getting gradually fewer.

### The selection of the 100th species

To this effect, it was decided to enlist the community of invasion biologists in selecting the new, 100th IAS for the list. As it would be difficult to get a meaningful consensus from a pool of tens of thousands of IAS species, we first selected a reasonable number of candidates among which the community was invited to choose. Following the same thinking behind the development of the original list, this approach was not meant to be an accurate and objective selection of the worst invaders, but rather a rational selection of some



**Fig. 1** Taxonomic representation of 100 of the world's worst alien invasive species

of the worst, as it is difficult to classify objectively and quantitatively one species as worse than another. We thus amassed invasive alien species inventories/checklists from 16 global and national databases, including the ISSG Global Invasive Species Database (GISD), CABI Invasive Species Compendium (ISC) and DAISIE (Delivering Alien Invasive Species Inventories for Europe), and selected over 10,000 IAS that we ranked based on the number of times they were listed. We then accounted for emerging threats, i.e., species that are not yet widespread but that are known to have major impacts and/or a high spread rate, so that they would rise in the ranking. We selected the first 50 species and assigned to each of them a score of (1) spread: the number of continents already invaded and (2) impact: ecological, economic and/or health. We finally eliminated the species in genera that were already represented in the 100-list, as well as those that had a strong positive value (cultural or economic). We then selected the 10 species with the highest sum of scores. These 10 species were six aquatic and four terrestrial organisms, five plants and five animals. They came from South and North America, Asia, Europe and Oceania and had strong ecological, economic and/or health impacts. They included organisms that are invasive throughout the world, such as the American waterweed *Elodea canadensis*, but also still localized but very fast spreading organisms, such as the lionfish *Pterois volitans*, or species with very high local impact, such

as the Burmese python *Python molurus bivittatus*. The address of a dedicated web site (Courchamp 2013) was distributed via various networks to the invasion biology community throughout a period of 3 months. The site included a description of the selection protocol, a short presentation of the 10 candidates and an explanation on how to vote online for the latest and 100th representative of the IUCN “100 of the worst” list. We used the Condorcet Vote, a procedure that selects the candidate (here a species) that would win by majority rule in all pairings against the other candidates (Courchamp 2013). It requires only one round of voting.

A total of 652 experts from 63 countries voted, and they selected giant salvinia, *Salvinia molesta*, as the 100th species to join the IUCN list of “100 of the world's worst invasive alien species”. It is a free-floating aquatic fern (Fig. 2) native to southeastern Brazil, first observed outside its native range in 1939. It has since spread widely throughout the tropics and subtropics across the world and is currently found in 31 countries on 4 continents (Fig. 2). This plant is moved in part by the trade in ornamental plants for fish tanks and ponds. The presence of giant salvinia is prominent in slow-moving, quiet freshwater systems. Its fast growth rate, under optimal conditions, enables this plant to double its abundance in only a few days. It forms 10–20 cm thick floating mats (Fig. 2) that prevent light penetration of the water column, reducing oxygen content and degrading water quality for



**Fig. 2** **a** Close up of *S. molesta*, **b** free-floating aquatic group of salvinia, **c** floating mats of salvinia in Australia, **d** records of salvinia worldwide collected from a variety of databases including GBIF (<http://data.gbif.org>), CABI ([www.cabi.org/isc](http://www.cabi.org/isc)), and IOBIS (<http://www.iobis.org>)

aquatic organisms, drastically damaging these ecosystems over large areas (Fig. 2). In addition, dense mats of salvinia can impede water-based transport,

reduce water quality, impair aesthetic values, clog irrigation and power generation intakes, and harm local fisheries (Julien et al. 2002). Maintaining giant salvinia at low levels is generally attempted by the use of herbicides, which are notoriously costly. Biological control programs can achieve local successes but have not controlled salvinia in other areas, nor prevented its spread (Room et al. 1984; Julien et al. 2002).

Although salvinia definitely deserves its place in the list, other species among the 10 candidates, and beyond, could have been selected instead. The new status of salvinia does not make it suddenly more invasive, more damaging or more rapidly spreading. Nor has the need to remove it from invaded areas, or to prevent new introductions, suddenly become more critical. However, a listing in this very special catalogue will surely grant this species some extra attention, which will help impede its establishment and spread from now on. Invasion biologists also expect and hope that this new addition to the list will draw public attention to the damage caused by IAS in general. The IUCN list of “100 of the world’s worst invasive alien species” is a potent communication tool. One of the expectations of the invasion biology community when building this list was, oddly, that it would help them to remove species from it, as often as possible. Control of alien invasive species, even eradication when possible, is crucial to preserve biodiversity and lower costs for human societies. However, although reactive programs are required, they remain far more expensive than proactive programs (Kaiser and Burnett 2010). Prevention, early detection, and rapid response are the three pillars of success, and this rest on effective communication.

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# Characterising current and predicting future ant invasions

Cleo Bertelsmeier and Franck Courchamp





# 4. Invasive ants

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## 4.1. Introduction

Ants had an enormous evolutionary success having colonised every landmass on Earth apart from Antarctica. Some estimates suggest that the 12,000 described species of ants account for up to 15-25% of terrestrial animal biomass <sup>1</sup>. They are conspicuous and dominant members of most terrestrial ecosystems and are often classified as key stone species or ecosystem engineers, since they shape in large part the structure and diversity of their habitats <sup>2</sup>. The abundance and diversity of ants is thought to stem from a successful way of living in societies with a coordinated division of labour. This cooperative social system is an asset not only in their native ecosystem but also in the context of new ecosystem colonisations and invasion. As human-mediated transports increase, ants are becoming major invaders in ecosystems that were previously beyond their geographical reach and are now among the most damaging invasive species <sup>3-5</sup>. Among them, five species are recorded in the “100 of the worst invasive species list” by the Invasive Species Specialist Group of the IUCN ([www.issg.org](http://www.issg.org)): The Argentine ant (*Linepithema humile*), big-headed ants (*Pheidole megacephala*), red imported fire ants (*Solenopsis invicta*), little fire ants (*Wasmannia auropunctata*), crazy ants (*Anoplolepis gracilipes*). In general, invasive ants have an immense impact on fauna and flora of the invaded ecosystem, killing even very large animals <sup>6</sup>. Because they play an important role they play in various ecological processes <sup>2,7-9</sup>, displacement of only a few native ant species by exotic ants can have disproportionate consequences for ecosystem functioning. In addition, ant pests are extremely difficult to eradicate because they are small, numerous and colonial. Economic losses can be high due to the destruction of cultures or managed forests, damages to technological structures and the invasion of human estates. For example, a single invasive ant species (*S. invicta*) is estimated to cost the United States one billion US\$ annually <sup>10</sup>.

Because of their high impacts on fauna and flora, invasive ants have received much attention in the literature, with a high number of studies over the past decade, at a rate that is currently accelerating. Amid the new wealth of this recent literature, there is a dire need for an up-to-date synthesis on this key ecological and conservation subject. Our aim is to provide such a critical review, starting by describing the direct and indirect ecological impacts of ant invasions. Then, we will summarize attempts that have been made to identify the key factors determining invasion success, including ecological traits of invasive ant species, abiotic conditions, biotic interactions and geographic patterns of introduction pathways. In the last part, we will review tools available for prediction of future ant invasions.

## 4.2. Impacts of ant invasions

Ants are keystone species in many ecosystems and once they become invasive they can have a variety of different direct and indirect impacts on biodiversity (Fig. 1).

### 4.2.1. Direct effects

Invasive ants can have a huge direct impact on a wide range of taxa, frequently causing their competitive exclusion and local extinction. They are known for their direct impacts on native ants through interference or exploitative competition<sup>12,13</sup> 14-16, on crabs through predation<sup>17</sup> or resource competition<sup>18</sup>, a variety of arthropods<sup>13,19</sup>, lizards<sup>20</sup>, on birds through nesting disruption<sup>21</sup>, on herpetofauna<sup>22</sup> and even on large mammals<sup>23</sup>. Extreme examples include elephants that can be blinded due to ulceration because of the sting of little fire ants<sup>24</sup>. These direct impacts of invasive ants and quantitative measurements of the decline of affected species have been discussed in great length in the literature; for a more comprehensive list of taxonomic groups that can be affected by invasive ants, see<sup>11</sup> and<sup>6</sup>. Even though the vast majority of affected species will experience negative effects, some may benefit from the presence of invasive ants. Yet, as we detail below, that may in turn have a negative indirect effects on other taxa and even seriously compromise numerous ecosystem processes.

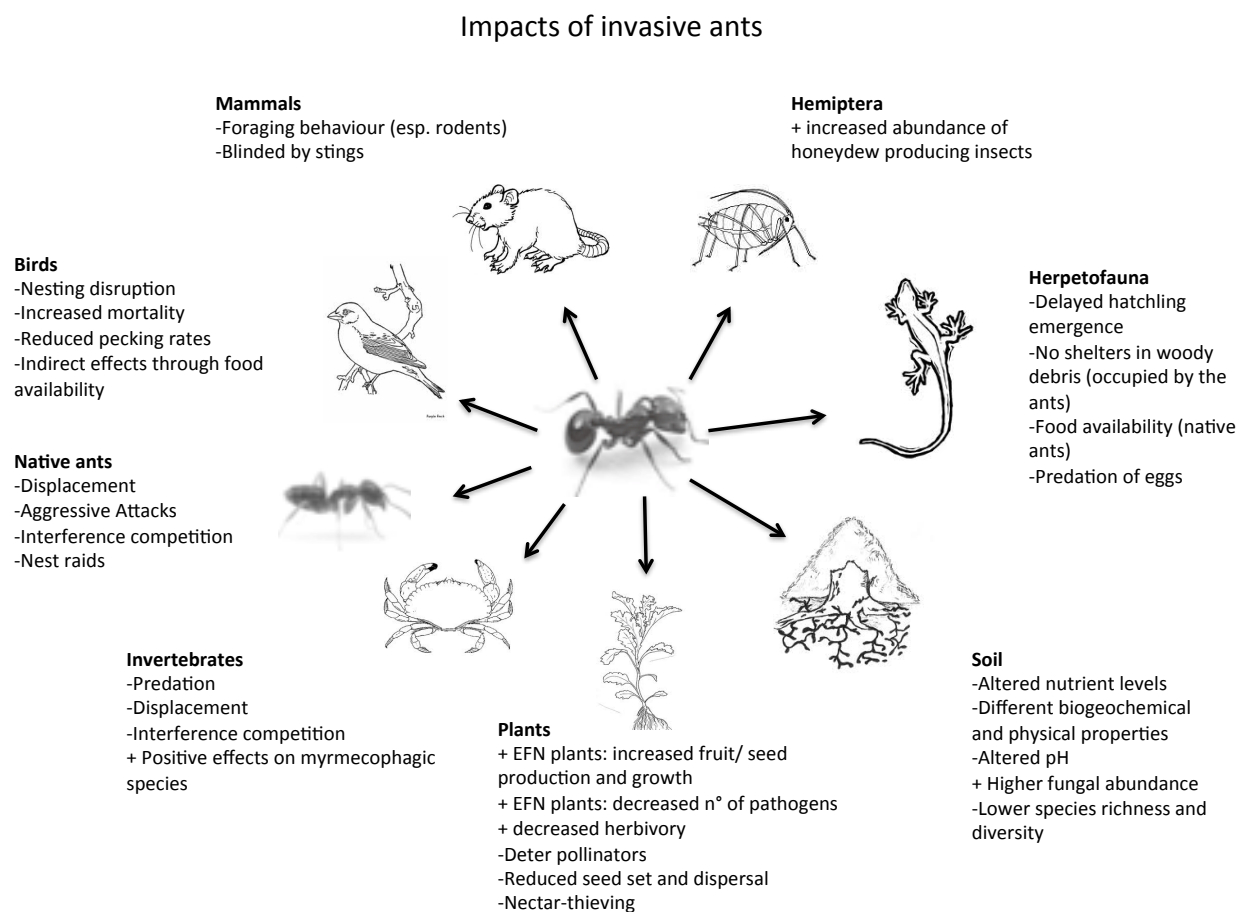


Fig. 1 Examples of impacts of invasive ants on biodiversity

#### 4.2.2. Indirect effects

##### *Seed dispersal*

One important ecological process that can be impaired by invasive ants is seed dispersal, which has negative consequences for a variety of plant species<sup>25</sup>. This can happen through different ways. First, some invasive ants species (*e.g.*, *S. invicta*, *S. geminata*, *W. auropunctata*, *P. longicornis*) can directly predate on seeds or consume the eliasome without moving the seed<sup>11</sup>. In addition, some invasive ants disperse seeds, but leave them exposed at the soil surface so that other granivores can consume (and disperse) them<sup>(11 and references therein)</sup>. Due to their generally small size, invasive ants (*e.g.*, *S. invicta*, *S. geminata*, *W. auropunctat*, *P. longicornis*) may also move seeds at a slower rate or over a shorter distance than the native species that have been extirpated by the invasive ants<sup>26,27</sup>. Impacts on seed dispersal by invasive ants can even facilitate the co-invasion of invasive plants. One study<sup>28</sup> examined seed dispersal of two native and two invasive plant species by *L. humile*) –at invaded or uninvaded sites in south-eastern Australia. They found that Argentine ants transported significantly more seeds of the invasive plants. As a result, Argentine ants generally can change the relative abundances of different plant species, favouring those which seeds are smaller and lighter<sup>29</sup>.

Moreover, invasive ants can erode seed dispersal by taxa other than ants. For example, the yellow crazy ant (*A. gracilipes*) disrupts frugivory of endemic seed dispersing birds on Christmas Island, Indian Ocean<sup>30</sup>. There, the ants directly interfere with the birds, reducing their pecking rate up to six fold.

##### *Pollination*

Invasive ants have negative impacts on flowering plants by displacing pollinators. It has been shown that dipteran pollinators visited fewer flowers in the invaded than in the uninvaded area<sup>31</sup>, leading to a reduced pollination rate and consequently to reduced fruit and seed set in the invaded area. Lach<sup>32</sup> suggests that exploring the competitive abilities of invasive ants relative to native flower visitors will be especially important in agricultural and other systems that are already nectar or pollen limited. However, another study found a decrease in floral arthropods following invasion by ants but could not find an effect on seed set on *Protea nidida*, a tree species native to the South African fynbos<sup>33</sup>.

##### *Nutrient cycling in the soil*

Invasive ants can greatly alter soil properties because the vast majority of them are ground-dwelling species. Mound or nest constructions of ants and their foraging activity thus modify the biochemical and physical properties of the soil<sup>8</sup>, changing soil textures, lowering bulk density and increasing infiltration<sup>9</sup>. Mound building activity of *S. invicta* increased nitrate concentration around the mound soil, but reduced concentrations of organic matter, phosphorus, magnesium, copper and zinc<sup>34</sup>. In some cases, plants may be able to benefit from increased nitrate concentrations<sup>35</sup>. It has also been shown that some species prefer the fine soil structure of ant mound soil<sup>36</sup>.

##### *Species positively affected by invasive ants*

Extra-floral nectar (EFN) plants generally benefit from the association with invasive ants because these ants are especially abundant and aggressive making them better plant

guards than native ant species. Some plants showed increased fruit or seed production, increased growth or decreased numbers of pathogens (<sup>11</sup> and references therein).

Plants hosting aphids also profit in some cases from the presence of invasive ants. A study found that Argentine ants reduced damage to plants due to skeletonising insects by 50% <sup>37</sup>. Likewise, the presence of *S. invicta*, attracted by the presence of cotton aphids, reduced caterpillar survival and herbivory, resulting in 16% more bolls, 25% more seeds and 10% greater seedcotton mass on cotton plants <sup>38</sup>.

Species that predate on invasive ants may also be positively affected by their presence. In Japan treefrogs, *Hyla japonica*, <sup>39</sup> and the myrmecophagic jumping spider, *Siler cupreus* Simon, <sup>40</sup> both prey on Argentine ants and their brood. The pit-building ant lion (Myrmeleon) that became heavier, had longer mandibles and grew more quickly when its diet consisted of Argentine ants instead of the native species <sup>41</sup>.

### Community structure

Resulting from their differential direct and indirect impact on various species, invasive ants alter competitive relationships between native species. For example, native ant communities in areas that have not been invaded by Argentine ants exhibit significant species segregation, consistent with competitive dynamics <sup>13</sup>. But within one year following the arrival of Argentine ants, ant communities exhibited random or only weakly aggregated patterns in species co-occurrence <sup>42</sup>. Another study has shown that the invasion by a generalist predator, the little red fire ant (*W. auropunctata*), can have an impact on both grazing and detrital invertebrate communities and ecosystem processes in a rainforest understorey <sup>43</sup>. The ants alter herbivore regimes and may indirectly alter litter decomposition and nutrient cycling in the soil by suppressing important microbivore and detrivore communities.

#### 4.2.3. Difficulties in assessing impacts of invasive ants

Most research papers assessing the role of ants on their invaded ecosystem base their conclusions on studies with only two species: *L. humile* and *S. invicta*. Only very recently, some studies investigated the impacts of *A. gracilipes*, *W. auropunctata* and *P. megacephala*. Most invasive species remain greatly understudied.

Another problem is that most studies on the impacts of invasive ants are observational or correlational. Because of inherent ethical problems of manipulating invasive species in the field linked to the risk of accidentally causing a real invasion <sup>6</sup>, there are very few attempts to explore the mechanisms of invasiveness in ants by carrying out experiments<sup>11</sup>. Knowledge of the effects of ant invasion comes mostly from observations of a decrease in local species richness and abundance. But it is often difficult distinguish between the impacts on biodiversity of invasive ants and those of confounding factors, such as disturbance. Therefore, it is often difficult to establish causal links between the invasion and changes in communities and ecosystem processes. King and Tschinkel <sup>45</sup> eliminated experimentally invasive populations of *S. invicta* and their results suggest that this invasive ant was not a superior competitor that suppressed native ants. The low diversity and abundance of native ants that was observed rather resulted from other factors, such as prior disturbance and recruitment limitation that may be the primary limiting factor for native species in these degraded ecosystems <sup>45</sup>.

In addition, different populations of the same invasive ant species can have very heterogeneous effects on similar ecosystems. For example, two populations of *A. gracilipes* invaded two different islands in the Nukunonu Atoll of Tokelau, Pacific Ocean, where they now show very different levels of both aggressiveness and density<sup>46</sup>. The higher (sevenfold) density population co-existed with 50% fewer other ant species.

Moreover, the impacts of invasive ants can vary over time, and the direction of the effect may be context dependent. Residence time of *W. auropunctata* at different sites in continental Africa was negatively correlated with the number of native ant species present<sup>47</sup>. On the other hand, native ant species returned 12 years after initial invasion of *S. invicta* in central Texas, although the invasive ant species was still the most abundant one<sup>48</sup>. Similarly, native ant species richness in areas in California invaded by Argentine ants increased significantly over 13 years of observation<sup>16</sup>. This suggests that the effects of the invasion might be most severe during the initial phases.

Furthermore, evolutionary changes should be taken into account when assessing the impact of invasive ants. The invader can show evolutionary changes when it is introduced into new environments that may change its impacts on native fauna and flora over time<sup>49</sup>. In addition, invaders can also exert selective pressures on native species. Within 70 years of the introduction of *S. invicta*, native lizards have been shown to use new anti-predator behaviours and have evolved altered morphologies that mitigate potentially lethal attack by these ants<sup>20</sup>.

Unfortunately, few of the factors above are taken into consideration in current studies of the ecological effects of invasive ants.

### 4.3. The keys of invasion success

As mentioned earlier, there are hundred of introduced ant species, and only a fraction of invasive species. Why then does a particular species become invasive in a particular place at a particular point in time? There are four broad categories of factors influencing whether or not an introduced species will become invasive. First, there is a certain number of ecological species traits that are thought to increase the probability of becoming invasive<sup>3</sup>. Certain traits might be a necessary pre-condition whilst others may be just beneficial to becoming an invader. The second category of factors that should be considered to find out whether a potentially invasive species is going to invade in a particular region, are abiotic characteristics of the ecosystem such as climatic conditions, habitat or soil type and the degree of disturbance. Third, invasions can benefit from positive biotic interactions such as facilitation, co-invasion or enemy release or may be hindered by biotic resistance of native species, competition among several invasive species or the absence of symbiotic species. Lastly, the introduction pathways and propagules pressure play a role, too. We will give a synthetic overview of the different determinants of ant invasion success from all of those different categories (Fig 2).

Factors determining invasion success of ants

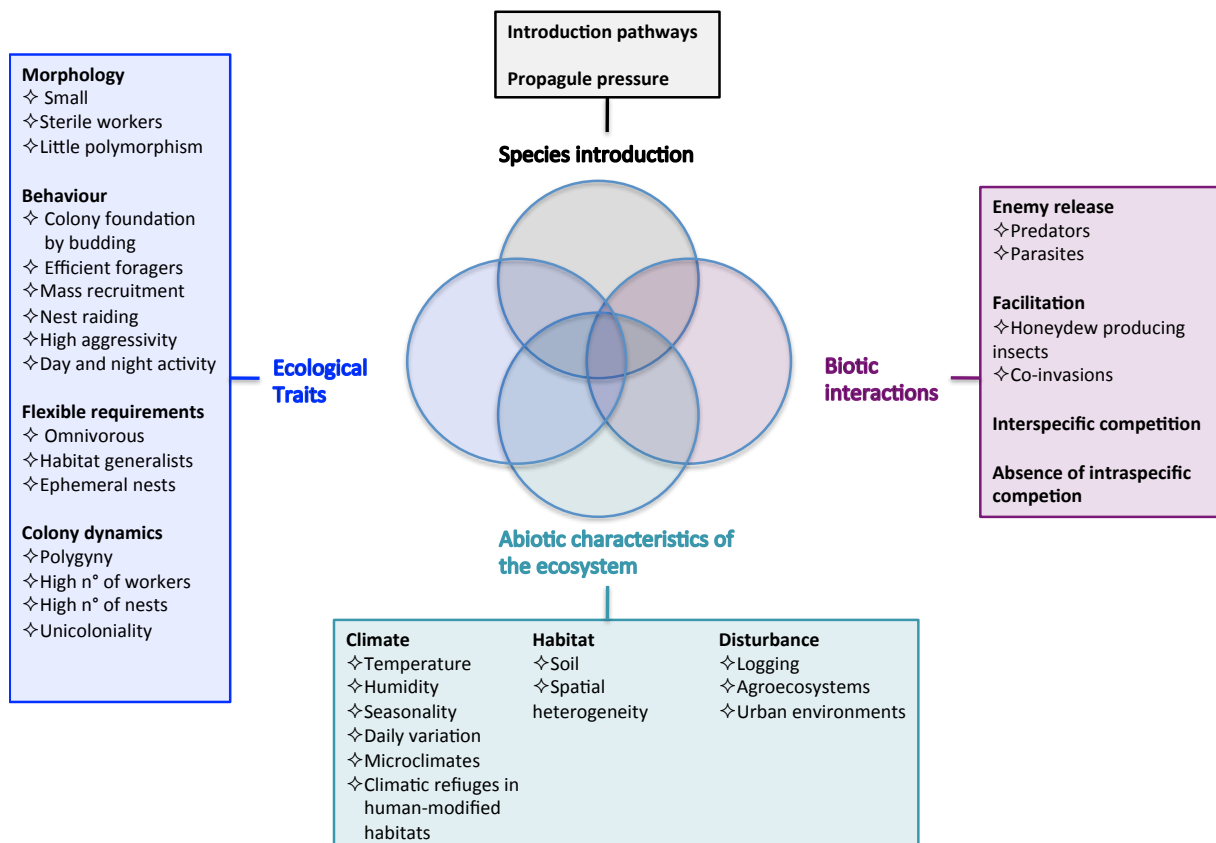


Fig. 2 Factors influencing the invasion success of ants

4.3.1. Characteristics of invading ants

Morphology

Worker size seems to play an important role for invasions <sup>6</sup>. Mc Glynn compared the size of 78 non-native species with the size of native congeneric species and found that the exotic ant species were smaller <sup>3</sup>, a pattern confirmed in another study investigating the size of exotic ant species in New Zealand <sup>50</sup>. This size relationship holds true even for intra-specific differences in native and non-native population of a single species, *W. auropunctata* <sup>3</sup>. Size may also play a role in the invasion success of *Lasius neglectus* which produces a high number of nanitics (small, fast developing workers) in addition to the “regular” workers <sup>51</sup>. The mechanism by which size affects invasion success remains to be elucidated, but it could also be due to an introduction bias because smaller ants may be more easily transported and less easily detected.

Behaviour

Invasive ants disperse by dependent colony foundation, or “budding”, during which a young fertilized queen disperses on foot from her maternal nest, taking with her a certain number of workers that help her during the initial stages of colony foundation <sup>6</sup>. Budding greatly limits the dispersal distance relative to dispersion by a nuptial flight, but may be advantageous to cover efficiently a new area.

Invasive ants may become ecologically dominant because of an efficient way to monopolize and retrieve food resources. For example, workers of *A. gracilipes* forage continuously over 24h<sup>17</sup>. Argentine ants have been noted for their aggressiveness and fast recruitment to a food source<sup>53</sup>. They also show higher activity levels than native ant species. In the invaded range, food was discovered more quickly by the invasive species than in the un-invaded range by non-invasive species, even though the total ant number was lower there<sup>54</sup>. In Mexico, *P. megacephala* workers can singly capture a wide range of insects and use mass recruitment with an alarm pheromone for very large prey<sup>56</sup>. As a result, workers of this species are significantly better at capturing termite workers than even the most successful native species<sup>55</sup>. Even though it is generally believed that high aggressiveness of the invaders is important for bait dominance<sup>14</sup>, it has been suggested that some species, like the Argentine ant, lose on individual one-to-one fights, suggesting a potential compensation through efficient mass recruitment. In addition, during 20-to-20 fights against the native *Tapinoma sessile*, Argentine ants cooperated with each other forming a small group, thereby creating a local numerical advantage over the other species, leading ultimately to a global numerical advantage<sup>53</sup>. This cooperative strategy could provide a mechanism by which the species can outcompete much larger and ecologically dominant ant species during the initial stages of the invasion processes during which the invader lacks a numerical advantage.

Although less well documented, it has been suggested that organized nest raiding may contribute to the extirpation of native ants. For example Argentine ants commonly raid colonies of harvester ants in coastal southern California<sup>26</sup>. *P. megacephala* also raids nests of other ant species in its native range in Cameroon and in the introduced range in Mexico<sup>59</sup>. Interestingly, only 3 out of 11 native species put up a strong resistance to these nest raids in Mexico, contrasting with 11 out of 12 native species studied resisting such raids in the native range of *P. megacephala*<sup>59</sup>.

#### *Flexible requirements*

A characteristic of invasive ants is that they have are generalists instead of specialists. For example, there are no known invasive species relying on a tight symbiosis with a single very localised species. Invasive ants are omnivorous with a wide diet. They often opportunistically scavenge dead animals, hunt small invertebrates and exploit plant and insect exudates<sup>6</sup>. In addition, they are often habitat generalists, occurring in forests, grasslands, riparian zones, shrublands, urban and agricultural areas. Furthermore, invasive ants often have ephemeral nests<sup>60</sup> and can adjust their trail networks in a flexible way<sup>61</sup> allowing them to nest in a variety of places, e.g. in the soil, in tree branches or even in human estates.

#### *Colony dynamics*

Invasive ants often have a polygynous colony structure, where multiple reproductive queens are present simultaneously in each colony<sup>60</sup>. Passera and Aron list several examples of highly invasive ants ranging from 3 queens per 1000 workers in *L. neglectus* to 63 queens per 1000 workers in *L. humile* (<sup>62</sup> and references therein). *Cardiocondyla obscurior* even has up to 18 queens for only a few dozens of workers<sup>62</sup>, but this species is generally considered as a low threat due to its tiny colony sizes and solitary foragers<sup>63</sup>. *S. invicta* are a special case among invasive ants as they possess two reproductive forms: monogynous and polygynous colonies. Both social forms occur in two separately invaded areas in Taiwan; one population initially contained polygynous and



monogynous colonies<sup>65</sup>. But during subsequent spread it was mainly the monogynous form that colonized new areas. It is possible that monogynous colonies disperse over longer distances, but that polygyny confers in advantage during human-mediated transport because having a high number of reproductive queens in one colony can increase the probability of propagules containing reproductive individuals when colony fragments are transported by humans<sup>60</sup>. Although polygyny is the reproductive feature that attracts the highest interest in recent research papers, other factors of their reproductive biology may be important. In Argentine ants, invasive success may be increased by the continuous presence of haploid eggs and the ability to produce male and female sexuals throughout the year<sup>66</sup>. In addition, their ability to replace mated queens quickly due to intranidal mating assures a continued presence of reproductives in the colony, making the presence of queens even unnecessary for the successful establishment of colony fragments containing brood<sup>66</sup>. Furthermore, in addition to having a central role in changing migration patterns and transporting certain species with a certain set of characteristics, human can also exert direct selective pressures over species. In introduced populations of *W. auropunctata*, male and female clonality was very frequent and this particular reproductive system seems to be under selection in human-modified habitats<sup>67</sup>.

A large body of literature suggests that a key factor determining ant invasion success is the high number of workers (<sup>62</sup> and references therein). Numerical dominance is generally a key element affecting competitive outcomes in ants and invasive species often have extremely large colonies and high nest densities<sup>68</sup>. A high number of nests was found in *A. gracilipes* and seemed to increase its invasion success<sup>17</sup>. For example, on Christmas Island, Indian Ocean, *A. gracilipes* reaches the highest densities ever recorded of foraging workers, with 2254 ants per m<sup>2</sup><sup>17</sup>. Oliver et al<sup>69</sup> suggest that a minimum threshold abundance may be necessary to enable invasive ants to monopolise exudate-producing resources. They propose a “facilitation threshold hypothesis” where a minimum abundance of invasive ants must be exceeded before behavioural dominance can drive abundance rapidly upwards through positive feedback. In Argentine ants, every measure of competitive performance increased with the number of workers<sup>70</sup>. A study using different colony sizes with 10, 100, 200 and 1000 workers found that propagule size was important in determining competitive success in the lab, where small propagules of *L. humile* were quickly annihilated by local ants<sup>71</sup>, (although the result was not confirmed in a comparable field experiment). Whether or not invasive ants in general have large colony sizes remains to be tested, as even the opposite results may have been found<sup>72</sup>. Similarly, the role of the number of nests in invasions remains unclear<sup>70</sup>.

High nest densities can be the by-product of the breakdown of intraspecific territoriality leading to the absence of aggression between different nests that behave like one cooperative unit, called supercolony. Almost all invasive ant species form supercolonies<sup>68 73 74</sup>, with the most prominent example being a supercolony over 6000 km along the Mediterranean coastline<sup>75</sup>, the largest cooperative unit ever recorded. In order, to explore how the absence of aggression relates to the capacity to outcompete native species, Holway et al performed a lab experiment in which they reared colonies of a native ant species, *Forelius mccooki*, with a pair of Argentine ant colonies that either did or did not behave aggressively towards each other<sup>76</sup>. When the two Argentine ant colonies did not exhibit intra-specific aggression, the native ant species foraged less actively, produced fewer eggs and had generally fewer living workers, demonstrating

that the presence of cooperating colonies can dramatically alter the impact of an invasive ant species.

Different introduction events can give rise to different supercolonies that are aggressive towards each other<sup>77</sup>. Each introduction represents a different genetic bottleneck event, reducing genetic and cuticular hydrocarbon diversity important for non-nestmate recognition. It has been hypothesized that the loss of nestmate discrimination was the origin of supercolony formation<sup>75</sup>.

However, recently the “bottleneck origin” of supercolonies has been contested by several lines of evidence<sup>78</sup>. For example, workers belonging to a single supercolony of *W. auropunctata* in Israel had distinguishable hydrocarbon profiles and after 4 months in the lab they diverged further, indicating a strong interplay of environmental based and genetic based effects on the recognition cues<sup>79</sup>. After 4 months, workers kept in the lab behaved aggressively towards members of their own supercolony, demonstrating that the absence of aggression in supercolonies cannot be the sole effect of low genetic diversity.

Furthermore, it seems that supercolony formation can result from mixing of genetically homogeneous and nonaggressive colonies, or initially aggressive colonies harbouring the most common recognition alleles. Vasquez and Silverman showed that genetic and cuticular hydrocarbon similarity was positively correlated with the probability that initially aggressive colony pairs of Argentine ants fused<sup>80</sup>. But genetic relatedness is not always the decisive factor determining the level of aggression. Behavioural assays of 14 different colonies of the pharaoh ant (*M. pharaonis*) showed very low levels of aggression between geographically and genetically even very distant colonies<sup>81</sup>. Similarly, in Argentine ants workers form the dominant supercolonies in California and Europe did not show aggressive behaviour towards the dominant supercolony in Japan<sup>82</sup>. Sunamura et al suggest that in this case, low aggression may be due to frequent intercontinental exchanges of workers between the supercolonies. On the other hand, it has been proposed that the single worldwide supercolony which has been confirmed using aggression tests between workers from dominant supercolonies in North America, Europe, Asia, Hawaii, New Zealand and Australia has descended from a single ancestral colony<sup>83</sup>. The supercolonies on different continents have diverged very little despite having established more than 100 years ago<sup>83</sup>. However, this only concerns the biggest dominant supercolonies, as a study showed that the invasive Argentine populations from Macronesian islands behaved aggressively against a smaller European supercolony (the Catalanian supercolony) but not against the main supercolony<sup>84</sup>.

Though it was initially assumed that in unicoloniality (i.e. the capacity to form supercolonies) is a derived trait that evolved after the introduction into new habitats, more recently native supercolonies of Argentine ants have been discovered<sup>85</sup>. Overall, the structure of native and introduced is the same, but the size of native supercolonies only ranges over 25-500m, which is several orders of magnitude smaller than that of introduced supercolonies<sup>85</sup>. Like in introduced populations, relatedness among nestmates was not significantly different from zero and at the same time genetic differences between different supercolonies were high at nuclear and mitochondrial markers, demonstrating that these native supercolonies are extremely close breeding units (<sup>85</sup> in *L. humile*, <sup>86</sup> in *L. neglectus*). Competition between different supercolonies seems to be high. It has been estimated that around 1/3 of native supercolonies in

Argentine ants are replaced each year <sup>87</sup>. This highly selective dynamics may help maintaining unicoloniality over evolutionary time (for a detailed discussion on factors maintaining unicoloniality over evolutionary time scales see <sup>88</sup>).

The similarity of social organization in native and introduced populations suggests that invasiveness did not evolve as a single and contingent event, and that native Argentine ant supercolonies have characteristics that makes them pre-adapted to invade new habitats <sup>89</sup>.

Although unicoloniality is generally associated with invasive ants, it has also been observed in a non-invasive species, *Formica paralugubris* <sup>90</sup>. This study provided evidence that unicoloniality can be maintained, although members of different nests had a different genetic make-up and were able to discriminate between nestmates and non-nestmates as shown by prolonged antennation bouts.

#### 4.3.2. Characteristics of invaded areas

Abiotic conditions are the first major factors shaping biodiversity, and allow species that are adapted to them to live there. An exotic species has to be introduced to a region where it finds favourable abiotic conditions in order to proliferate and to become invasive. Climatic conditions in particular can influence the spread of an invasive species at a local scale, for example due to interannual variation in rainfall which was a good predictor of regional dynamics of the invasion front <sup>16</sup> and ultimately the rate of invasion <sup>92</sup>. For example, experimental *L. humile* nests under different temperatures in the lab will collapse if the soil temperature is below 5°C for more than 8 days because the ants cease foraging at this temperature and end up starving to death <sup>94</sup>. This estimation coincides with the observed patterns of *L. humile* invasion in the United States that is thought to be limited by winter soil temperatures <sup>94</sup>. Further features of the species' biology are temperature-dependent. For example, oviposition rates are optimal at 28°C and completely cease below a given temperature threshold <sup>95</sup>. In addition, different developmental stages (eggs, larvae, pupae, adult production) have different minimum and maximum temperature thresholds <sup>96</sup>. This is an important factor for determining invasion success, because the colony has to complete at least one colony cycle in order to establish. However, approaches determining upper or lower lethal temperatures of invasive ants in the lab <sup>97</sup> are of limited utility when making predictions of suitable habitat because the soil temperature experienced by the ants can be very different from the surface temperature <sup>98</sup>. For example in deserts where ants nest in the cooler soil belowground and survive although the surrounding temperature exceeds their lethal temperature. Moreover, many invasive ants are noted for their high ability of relocating their nests and altering foraging networks in a flexible way in order to adjust temperature and humidity conditions <sup>61</sup>. This temporal and spatial fluidity in colony structure is thought to constitute one of the keys of the invasion success in many ant species <sup>60</sup>.

In addition, when assessing invasiveness of a particular region, fine-scale variation in microclimatic conditions should be taken into account. Human-modified habitats often create abiotic conditions very different from the large-scale patterns. For example, agriculture can affect moisture levels which have been shown to be important determinants of Argentine ant invasion success <sup>99</sup>. Similarly, urbanization has led to

urban heat islands as much as 12°C hotter than their surroundings<sup>100</sup>, offering opportunities for exotic ants adapted to a warmer climate. Some studies have suggested that invasive ants are more susceptible to extreme climatic conditions than native ants of the invaded habitat and might depend more on favourable microclimatic conditions<sup>101 102</sup>. However, others hold an opposing view and suggest that the ability to withstand harsh conditions may be under selection after the introduction to a new habitat. Invasive populations of *W. auropunctata* survive colder temperatures and lower rainfall than native populations<sup>103</sup>. It is also possible that invasive species have a high phenotypic plasticity allowing them to acclimate better to the climate in the introduced range. A laboratory study has shown upper and lower lethal temperatures to vary by several degrees after a period of previous exposure<sup>104</sup>.

Yet, invasive ants may not experience the same climatic conditions as native ants, even in the same habitat. In some cases, native and non-native ants have different temporal niches and switch dominance according to seasons. For example on Okinawa Island, Japan, seasonal activity patterns were different between exotic and native ants, the native species being dominant only in spring and summer<sup>105</sup>. On a daily basis, dominance of invasive ants can change with temperature, too. In Western Australia *L. humile* can displace native ants from food baits only in the morning<sup>102</sup>.

Future climate change may exacerbate this problem causing increases of the current range of invasive species by lifting thermal barriers that for now confine them to warmer regions. For example, projections of potential suitable habitat of Argentine ants show a contraction of their range in the tropics but an expansion at higher latitudes under a scenario of climate change<sup>106</sup>. However, global models assessing the risk of ant invasions following climate change remain very scarce. It would be interesting to be able to compare the most threatening invasive ant species and the risk they are likely to pose for different regions of the world (Chapters 5-10).

#### *Disturbance and human impacts*

Ant invasions frequently take place in disturbed and human-modified habitats. Agricultural practices can influence the spread of invasive ants. For example, logging and other forms of natural resource extraction have increased 60 fold the rate of spread of *W. auropunctata* into inner Gabon<sup>23</sup>. Monitoring of the ant community immediately after clear-cutting forest in South Carolina revealed that *S. invicta* and *Pheidole* ssp. invaded the newly disturbed sites very rapidly post-cutting<sup>107</sup>. Anthropogenic habitat modification such as tree management in agroecoforests can also promote the spread of invasive ants. For example *A. gracilipes* was frequently found in Indonesian cacao agroforests and its presence was associated with decreased forest ant species richness<sup>108</sup>.

Disturbance may also promote ant invasions indirectly. A model of the evolution of dispersal strategies predicts that disturbance should favour budding as a dispersal strategy because disturbance is assumed to increase colony mortality<sup>109</sup>. The alternative winged dispersal would be disadvantageous because single queens found their colony alone and have a very low probability of successfully establishing a nest in a disturbed habitat because they are alone<sup>109</sup>. By selecting species that disperse by budding, disturbance indirectly favours invasive species because among those budding is the predominant mode of colony foundation. Moreover, human modified habitats may have selected for male and female clonality in invasive populations of *W. auropunctata*,

illustrating that humans do not only disperse species but also exert selective pressures over invasive species <sup>67</sup>.

Although disturbance appears to be frequently an important factor favouring ant invasions, some exceptions have been recorded <sup>110,111</sup>. Plowes et al <sup>112</sup> found that *S. invicta* has invaded natural habitats and displaced native ant species, which have found refuges in adjacent residential areas where the invasive species did not establish.

A large-scale field experiment showed that disturbance greatly decreases native ant species richness in the absence of invasive species whereas invasive ants alone without disturbance had a much lower impact on native ants <sup>113</sup>. This indicates that in many instances invasive ants may benefit from disturbance but are not the main driver of species loss. In agreement with that view, Roura-Pascual et al. <sup>111</sup> found that land use *per se* does not determine the rate of spread of Argentine ants which is rather due to the effect of human-modified habitat on native ant communities and abiotic suitability of the site.

#### *Biotic interactions*

One of the common hypotheses to explain invasion success is the “Enemy Release hypothesis” whereby in the invaded range the introduced species is released from the pressures its natural enemies (e.g., predators or parasites) normally exert and consequently shows a demographic explosion <sup>17</sup>. Results supporting this hypothesis have been found in many taxonomic groups, including ant species. A study investigated the presence of 6 microbes in recently established populations of *S. invicta* on several continents and found that only two of the microbes were present in the invaded range. The Enemy Release hypothesis probably facilitates many invasions, but probably never is the unique reason for success. It may for example operate in conjunction with lower intra-specific aggression and higher worker efficiency in the case of the *A. gracilipes* invasion on Christmas Island <sup>17</sup>.

Facilitation, for example through the association with honeydew producing insects, is another important biotic interaction during invasions <sup>33,69,114-117</sup>. The availability of carbohydrate sources can favour ant abundance and spread <sup>116</sup> as well as colony size <sup>115</sup>. It can also increase patrolling behaviour in workers and lead to lower colony mortality and higher final colony sizes <sup>117</sup>. In fact, honeydew is such an important food source that it can affect behaviour, leading to altered competitive dominance relationships. Colonies of Argentine ants became less aggressive and less active when they were reared on a diet of insect prey only, deprived of honeydew <sup>114</sup>. Given the important role of honeydew for invasive ants, it is not surprising that they seem to be better at tending Hemiptera and collecting honeydew than native species <sup>118</sup>.

In some cases, the invasion of an ant species has even been facilitated by an invasive mutualist, leading to a co-invasion. It has been estimated that honeydew produced by Homoptera supplies half of the daily energetic requirements of a *S. invicta* colony and 70% of that come from only one species of invasive mealybug, *Antonina graminis* in Texas <sup>119</sup>. Although co-invading Homoptera remain largely unstudied, they could be important in numerous ant invasions <sup>119</sup>.

On contrary, interactions with other invasive ant species can be a factor hindering invasion success. For example, behavioural assays have shown that *A. gracilipes* attacks,

kills and repels foraging *S. invicta* workers at baits where they co-occur<sup>123</sup>. Both species are present in different regions of China and *A. gracilipes* might limit the future spread of *S. invicta* if they compete for the same food resources in the field. Two invasive species that co-occur in their native habitat, *L. humile* and *S. invicta* display an invasive syndrome in their native range. Here, strong interspecific competition is likely to be an important limiting factor<sup>124</sup>.

#### 4.3.3. Geographic patterns and introduction pathways

Although ants are rather poor long-distance dispersers, recent increase in human commerce and tourism has transported over 200 species all over the world<sup>125</sup>. Before ants had been unable to colonize many mid-Atlantic and Pacific islands. For example, Hawaii has no native ant fauna but today there are more approximately 50 ant species, introduced mostly during the 20<sup>th</sup> century<sup>126</sup>. The vast majority (>90%) of ant species introduced to the US occur on plants, mostly on orchids and bromeliads and some on fruits, other ornamental plants and Acacia trees<sup>127</sup>. Ants have been exported from and imported to all major biogeographic regions, but the Oriental and Neotropical regions have exported more species than they have received<sup>128</sup>. But as little information exists on invasions in Africa and as ant sampling is strongly biased across regions, it remains unclear to what extent this pattern reflects geographical biases in studies (<sup>125</sup> and references therein).

More recently, studies have been focusing on retracing the invasion history of some of the worst invasive species, inferring the number of introduction events and the number of native sources using genetic markers<sup>60,73,81,89,129</sup>. For example, an analysis of the introduction history of *S. invicta* at a global scale using molecular markers from 75 geographic sites worldwide revealed that at least 9 introductions have occurred into newly invaded areas and that all but one have been secondary introductions from the main one in the Southern US<sup>130, 129</sup>. Similarly, global invasion histories have been analysed in *M. pharaonis*, which been introduced separately at least 34 times on 4 continents<sup>81</sup> and in *L. humile*, which has been introduced at least 14 times<sup>89</sup>.

Behavioural assays are a complementary way to study introduction histories. Within a supercolony derived from a single native source, population individuals do not behave aggressively towards each other, allowing investigating whether different supercolonies have originated from the same native supercolony. For example, three mutually aggressive supercolonies exist in one port in Japan, providing evidence – in conjunction with genetic analyses - for multiple invasions of distinct source populations into a base of international trade<sup>77</sup>.

#### 4.3.4. Difficulties in determining factors influencing invasion success

Elucidating the key mechanisms of ant invasion success in general shown recent progress but the vast majority of studies concentrate on only 2 species, *L. humile* and *S. invicta*. Basic information is lacking on most other invasive species, even the most ecologically threatening of them. In addition, the great majority of articles on characteristics of invasive ants concerns only one of them, supercolonies. Yet, even

though a certain number of traits are believed to be associated with ant invasions, most other ecological characteristics have been so far overlooked, to the point that many are undocumented for many invasive species. So far, only propagule pressure<sup>127</sup>, nesting behaviour<sup>127</sup> and body size<sup>3</sup> have been tested for their statistical significance. Moreover, research has largely focused on the characteristics of introduced populations of invasive ants. But it would be very interesting to know more about native populations in order to determine whether invasiveness has evolved through a genetic bottleneck or selective pressures after introduction. Or, alternatively, if species are pre-adapted to becoming invasive presenting already traits that could make them invasive. Obviously, there has not been a quantitative assessment that compares the frequency of these traits in invasive ants to their frequency in native ants, although such study would be very fruitful in this field.

## 4.4. Prediction and management of ant invasions

### 4.4.1. Management of ant invasions

As for all invasive species, preventing introduction is by far the best course of action to avoid invasions. The probability to eradicate invading ants is highest during their earliest stages of invasion. Therefore careful monitoring of ports of entry and ecological surveys can be critical. Once ants have invaded a new habitat, it becomes a very challenging task to eradicate them because killing foragers will eliminate only a small fraction of the colony with little or no impact on the overall colony dynamics<sup>132</sup>. Moreover, the toxic compound shouldn't kill the worker instantaneously because it has to be delivered to the queens. Furthermore, successfully removing single colonies is pointless in the case of supercolonies. Currently, there is no universally effective treatment product available (<sup>132</sup> and references therein). The ineffectiveness of the elimination of small parts of the supercolony of Argentine ants triggered calls for more aggressive eradication strategies to avoid quick re-infestation, either using more specifically attractive baits<sup>134</sup> or giving up toxic baiting altogether<sup>133</sup>. Alternative eradication strategies include exclusion techniques, insecticidal spray and habitat modification<sup>135</sup>. Despite improving methods, eradication success remains rare (but see<sup>136</sup>).

### 4.4.2. Predicting invasions

Recently, a large body of literature has developed on how to predict future ant invasions and to identify suitable habitat for species that are already known to be invasive.

#### *Species distribution models*

One method to predict potential suitable habitat for invasive species are species distribution models. Coordinates of the species' current distribution are correlated with environmental – mostly climatic – variables, in order to define the species' climatic niche or “bioclimatic envelope”<sup>137-139</sup>. These models make the assumption that the species current distribution reflects its ideal environmental requirements and look for such ideal conditions in different places or different times. Typically, this bioclimatic envelope can be projected onto a climate map in order to identify suitable ranges where the species is not present so far, but would invade successfully if introduced there.

Alternatively, it is also possible to work under a scenario of future climatic conditions, which allows to explore the potential invasive range under global climate change. A certain number of studies has used these correlative species distribution models to explore the current potential range of invasive species<sup>140 141 142 143 144</sup>. But, as these invasions are currently and will increasingly take place under changing climate, it is surprising that few studies considered these future climatic conditions. This is especially so since climate change is widely recognized as a major factor determining species' distributions in the future<sup>145</sup>. A study on Argentine ants predicts that its potential range retracts in tropical regions but expands at higher latitude areas by 2050 under a scenario of climate change<sup>106</sup>. However, predictive maps should be viewed as mapping the range of habitat that presents a certain number of the species' abiotic requirements, rather a concrete forecast of species invasions. Indeed, niche models include implicit assumptions and methodological limitations that constrain their predictive power. Range predictions vary with the variables considered to model a species' niche<sup>146</sup>, with the environmental data sets<sup>144</sup>, with the quality of the species distribution dataset, with the spatial and temporal scales<sup>147</sup> and with the correlative statistical methods<sup>141,148</sup>. In particular, the scale of climatic data from weather stations is not entirely compatible with the scale at which ants find favourable microclimatic conditions<sup>98,149</sup> (including in cities or other human-modified habitats). Furthermore, correlative niche models do not take into account biotic interactions, dispersal capacities and phenotypic plasticity or evolutionary adaptation and niche shifts<sup>142,143,150,151</sup>, all of which are decisive for ant invasion success or failure.

Despite these shortcomings, niche models still provide an important tool as a coarse assessment of whether or not an ant species is likely to invade a certain region. Considering the high number of very damaging ant species, it would be important to compare their potential to invade further regions, especially in the light of global climate change. Identifying the species that pose the greatest risk could help targeting for prevention efforts.

#### *Mechanistic models*

Mechanistic models aim to increase biological realism by basing spatial projections on physiological, genetic or demographic data that help estimate the ideal climatic conditions for a species. For example, Hartley and Lester<sup>152</sup> developed a model based on developmental rates at different temperatures, using an experimentally characterised threshold temperature of colony growth. The resulting cumulative "degree-day model" estimates the number of days above that threshold needed to complete the colony life cycle. It also takes into account faster rates of development at higher temperatures, up to a certain limit. Using maps of soil temperatures in New Zealand, sites that fulfil the minimum temperature requirements on an annual basis could then be identified. However, it has been argued that this degree-day model overestimated the potential range of that species and that another mechanistic model, this based on brood survival and oviposition rates at different temperatures, yields more precise predictions<sup>153</sup>.

Another ecophysiological model used minimum and maximum daily temperatures to predict the production of sexuals in *S. invicta*<sup>154</sup>, based on an earlier study that estimated the minimum number of 3900 alates needed to ensure a given colony reproduction success<sup>155</sup>. A minimal precipitation condition was added to the temperature-based projection by superposing a map with sufficient rainfall for colony



survival <sup>154</sup>. The resulting global map of potential habitat identified many areas in Europe, Asia, Africa, Australia and numerous islands as being currently at risk of *S. invicta* invasions. Applying this model to a scenario of climate change yielded an estimated range increase of 5% by 2050 and of more than 21% by the end of the century <sup>156</sup>.

The main limitation of mechanistic models is that they need a lot of data to yield biologically relevant predictions. Furthermore, the effect of climatic variables can differ at different life stages and by measuring variables such as oviposition temperature <sup>95</sup>, foraging at different temperatures <sup>157</sup> or upper lethal thermal limits <sup>104</sup>, one may still miss the relevant limiting factor that determines the distribution of the species. Because of the data requirements for physiological models, it is very difficult to envision a comparative approach, assessing the relative invasion risk of many ant species.

### *Spread models*

Spatially explicit spread models predict invasion dynamics from a point of entry, based on different modes of dispersal: colony budding, nuptial flights and long-distance dispersal during human mediated jump transportation. The latter is 2 to 5 orders of magnitude greater than local dispersal in *L. neglectus* <sup>158</sup>. Accordingly, global spread models can comprise two different linked models, one simulating local dispersal and one for long distance transport to estimate the rate of invasion and to pinpoint areas at particular risk <sup>161-163</sup>. The spread model can be calibrated with observed historic spread of the species.

Dynamics at the invasion front have been simulated using reaction-diffusion models <sup>159</sup>. It has been suggested that known dose-response establishment curves that estimate the propagule pressure needed for the species to colonize a new area should be incorporated in spread models <sup>160</sup>.

Spread models estimating a probability of presence at a particular location could be used to direct surveillance efforts at areas particularly at risk. Considering the eradication programme of *S. invicta* around Brisbane, Australia, it was calculated that more than twice as many fire ant nests could have been found in using this spread model compared to random searches. This might improve significantly the chances to eradicate the species <sup>163</sup>.

Spread models can be a complementary approach to niche models, for example by identifying probable points of entry within at-risk suitable areas that can be identified by a niche model <sup>164</sup>.

### *Experimental evidence*

Lab and field experiments can provide complementary evidence of the likeliness of an ant species to survive, establish and spread under a given set of conditions (both abiotic and biotic). Experiments are also important to provide physiological data that can be fed into mechanistic models <sup>95-97,104</sup>. They can also be used to test how the invasibility of a certain area changes with different human impacts <sup>113</sup>, i.e. different irrigation regimes in agricultural areas <sup>99</sup> or clear-cut logging <sup>107</sup>. Choice experiments are well suited to establish the ideal preferred conditions of a species <sup>93</sup>. Furthermore, experiments assessing the effect of colony size on its potential to persist and rear sexual brood and on

its growth rate are important to estimate the propagule pressure needed to invade a new habitat <sup>71</sup>.

Once suitable or preferred abiotic conditions have been delimited (*e.g.*, temperature), experimental approaches can also be used to identify potential invasion resistance from the local species. For example, behavioural dominance experiments can be used to establish hierarchies between different ant species in order to predict whether some native species are likely to resist a potential invasion of their habitat <sup>53</sup>. The dominance matrix established by these fight experiments or resource monopolisation experiments can also help predict which invasive species will eventually dominate over the others in cases where several invasive species are predicted to overlap in time and space <sup>165</sup>.

Overall, there are few field experiments owing to the inherent difficulty of performing experiments with invasive organisms, both logistical and ethical (but see <sup>113</sup> and <sup>71</sup>). However, it has been suggested that queenless colonies could serve as a model to investigate the effect of environmental conditions on the survival of Argentine ants <sup>94</sup>. Alternatively, invasion risks can be minimal if the experiment is carried out near the invasion front or if secured experimental nests are used which confine the queens <sup>71</sup>.

#### *Using characteristics*

Known characteristics of invasive ants can also serve to identify species that could become invasive in the future <sup>50</sup>. However, statistical predictions of the probability that a given species is going to become invasive knowing its set of ecological characteristics is currently hindered by a lack of knowledge about ecological traits in ants in general <sup>3</sup>.

Ward et al. <sup>166</sup> have developed a score-card approach to estimate invasion risks that can be applied to any region of interest ranking species according to the risk they pose. The score-card is designed to help decision-makers chose species for preventive efforts.

## 4.5. Conclusion

Ant invasions are increasingly recognised as a widespread, major ecological and conservation problem. In addition to causing great damages to native fauna and flora in various ecosystems on all continents, they incur very high economic costs to agriculture, forestry, real estate, health and tourism industries.

Until recently, most studies on the invasion process and the impact of invasive ants remained descriptive or correlational, but a tendency is slowly emerging to find mechanisms by which native species are displaced. Global comparisons of the impacts of invasive ants across their introduced ranges may help to elucidate how different environmental conditions and communities affect their biology and impacts <sup>11</sup>.

Analysing the keys of invasion success is a complex task, involving the investigation of ecological traits underlying the invasion success, abiotic and biotic factors alike, as well as understanding the dynamics of human-mediated transport. Some characteristics of species can change during or shortly after the invasion, due to genetic bottlenecks, phenotypic plasticity and evolution. It is important to compare native, exotic and invasive populations in order to investigate whether invasive traits are pre-adaptations

to invasion or are due to introduction biases or constitute traits that increase the success of invasive ants in achieving ecological dominance in the invaded habitat.

As for many other species, preventing ant invasions is better than eradicating them, especially since ant eradication programs are far from as efficient as for other taxon such as mammals. Therefore correlative niche models, mechanistic physiological models and spread models are of major importance, as valuable tools for assessing invasion risks. They all have a certain number of limitations that need to be considered carefully. Some may even prove to be of limited use for invasive species (that may not conserve their niche) or small organisms (which distribution could be determined by microenvironments rather than large-scale environmental data). However, available modelling techniques are very complementary and can still provide important approximations to whether or not a species is likely to invade in a certain area. They can in many cases be nicely completed by experimental approaches.

Despite the widely importance of ant invasions in many regards, the vast majority of research articles concentrates on a few species, mainly *L. humile* and *S. invicta*, when hundreds are already recognised as invasive somewhere in the world, and 19 are recognized as extremely problematic ([www.issg.org](http://www.issg.org)). Similarly, although unicoloniality and polygyny are well studied, especially for the two aforementioned species, basic ecological information for many important invasive species is still lacking. More knowledge on a wider range of species could enable us to use increasingly quantitative and comparative approaches, increasing our understanding of factors governing causes and consequences of ant invasions.

Finally, despite an increasing number of studies on invading ants, very few are currently examining them in a context of global change. Because they are the conditions in which invasions will occur and evolve in the future, it is crucial to multiply the very few studies taking into account climate and land use changes. Biological invasions and global climate change are listed among the “Top 5” factors threatening biodiversity. However, most species extinctions are likely to be due to an interaction between them. Therefore it is of uttermost importance to get a global picture of ant invasions in the future.

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# Climate Change May Boost the Invasion of the Asian Needle Ant

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# Climate Change May Boost the Invasion of the Asian Needle Ant

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## Abstract

Following its introduction from Asia to the USA, the Asian needle ant (*Pachycondyla chinensis*) is rapidly spreading into a wide range of habitats with great negative ecological affects. In addition, the species is a concern for human health because of its powerful, sometimes deadly, sting. Here, we assessed the potential of *P. chinensis* to spread further and to invade entirely new regions. We used species distribution models to assess suitable areas under current climatic conditions and in 2020, 2050 and 2080. With a consensus model, combining five different modelling techniques, three Global Circulation (climatic) Models and two CO<sub>2</sub> emission scenarios, we generated world maps with suitable climatic conditions. Our models suggest that the species currently has a far greater potential distribution than its current exotic range, including large parts of the world landmass, including Northeast America, Southeast Asia and Southeast America. Climate change is predicted to greatly exacerbate the risk of *P. chinensis* invasion by increasing the suitable landmass by 64.9% worldwide, with large increases in Europe (+210.1%), Oceania (+75.1%), North America (+74.9%) and Asia (+62.7%). The results of our study suggest *P. chinensis* deserves increased attention, especially in the light of on-going climate change.

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## Introduction

Among the over 12,000 described species of ants [1], more than 200 species have established populations outside their native range [2]. The rate of new species introductions continues to increase due to the ever growing human-mediated transportation via international trade and tourism [3]. Only a small subset of introduced ant species eventually becomes invasive, but these species can have a large impacts [4–6]. They can cause significant biodiversity losses, in particular as extremely efficient predators and competitors [7]. For example, most native ant species may be eliminated from the invaded habitat and a variety of other taxa, ranging from soil microbes to small mammals, can be negatively affected [6,8]. In addition, invasive ants can disturb ecological networks, such as seed dispersal mutualism, thereby impairing ecosystem functioning [7]. Finally, they often damage agroecosystems and are a nuisance to humans by infesting estates, leading to high economic costs [9].

Ants are known to be very sensitive to changes in temperature and humidity, because it affects their survival [10], foraging activity [11] and foraging networks [12] and dominance hierarchies [13]. It is generally accepted that with climate change, many invasive ant species will progressively colonize higher latitudes and altitudes, where the currently too cold climatic conditions are expected to become more suitable [14,15]. In this regard, several studies have used species distribution models [16–19] or physiological experiments [11,20,21] to investigate the relationship between temperature and humidity and ant distribution. Climate is one of the most important factors influencing the distribution of ants [22–24] and climatic suitability has been shown to be even the

most important factor responsible for the current global distribution of the invasive Argentine ant, *Linepithema humile* [25]. Climate can therefore serve as an important proxy to estimate the potential distribution of invasive ants worldwide. It is generally recognized that climate change is going to be a major determinant of species physiology, phenology and range shifts during this century [26]. However, few studies have gone beyond the estimation of current potential invasive range and forecast also the future potential distributions of invasive species in general (but see [27–29]). Furthermore, such pioneer studies estimating the future potential ranges of invasive ants have concentrated on the few species of *Linepithema humile* [25,30] *Solenopsis invicta* [31] and *Pheidole megacephala* [16], leaving a great knowledge gap for most other major invasive ant species.

Risk assessments conducted prior to the arrival of an invasive species are a vital component of biosecurity preparedness, because most species, including invasive ants, are extremely difficult to eradicate once they become established [32]. Providing a spatial model of relative climatic suitability is an important component of risk assessments to prioritize surveillance efforts for invasive species with a high likelihood of establishing in a particular region. The greater the extent of an invasion, the higher the environmental impacts of management attempts and the difficulty of achieving successful eradication [33]. It is known that reactive programs have generally a higher cost than proactive programs [34]. In this context, the Asian needle ant, *Pachycondyla chinensis*, is of utmost interest. Despite its introduction from Asia to the eastern part of North America in the first part of the 20<sup>th</sup> century, the invasion of this fast-spreading species was only detected recently in a wide

range of habitats in North America, including mature temperate forests, where it causes a strong decline in native ant abundance [35]. In addition, the species has been shown to disrupt an ant-seed dispersal mutualism by displacing a native keystone ant species [36]. The species' negative impact on native seed dispersers has been compared to the impact of Argentine ant [36], which is among the "100 of the worst invasive species" list of the IUCN [37] and has enormous impacts on biodiversity [38]. Additionally, *P. chinensis* is a growing concern for public health due to its powerful, and sometimes deadly, sting [35].

Consequently, there is a strong need to develop predictive models of the potential distribution of this highly invasive species, both currently and in the future with predictions of climate change. Here we use species distribution models to: (1) to quantify the current potential distribution worldwide and within six broad geographic regions; and (2) quantify the change in potential distribution with global climate change at the global and regional levels.

## Materials and Methods

### Species Distribution Data

Species distribution models search for a non-random association between environmental predictors and species occurrence data to make spatial predictions of potential distribution. Because our models should include the full set of climatic conditions under which the target species can exist, we included occurrence points (presence only data) from both invaded and native habitats [39]. In total, we used 283 occurrence points, 219 from North America (invaded range) and 64 from Asia (native range) (Fig. S1). The exact distribution of *P. chinensis*' native range is problematic as this species belongs to a large and taxonomically unresolved complex of species [40]. To maximize data integrity, the data used for modeling were limited to specimens collected in its native range and identified by one of the authors (BG) and specimens strictly identified as *P. chinensis* in literature [40,41]. In its introduced range, where *P. chinensis* identification is not problematic, localities were extracted from literature, museum records and personal collecting (BG).

For models requiring absence data, 10,000 pseudo-absence (background) points were generated randomly from all around the world to provide background data. This is a classic procedure because confirmed absence data is difficult to obtain for most species and requires great sampling efforts [42]. True absence data might improve the model accuracy because some pseudo-absence points may be drawn from regions where the species is actually present, but has not been recorded. However, it is not possible to base our projections on true absences due to lacking large-scale absence data of the species. In addition, in the case of invasive species, even a true absence point may indicate a suitable location that the species has not yet been introduced to due to a lack of opportunity. Therefore, we believe that pseudo-absence data can serve as a reasonable proxy.

### Climatic Predictors

Climatic predictor data was sourced from the Worldclim dataset. The 19 Worldclim variables represent annual trends (e.g. mean annual temperature, annual precipitation) and extreme limiting environmental factors (e.g. temperature of the coldest and warmest months, precipitation of the wettest or driest quarter) and are known to influence species distributions [45,46]. All Worldclim variables are 30-year averages of monthly temperature and rainfall values from 1960–1990 [43], which is characteristic of the climate that the species experienced when the occurrence point was

collected or the species established in this locality. We modelled the species niche based on 4 of the 19 bioclimatic variables that were not collinear (pair-wise  $r_{\text{Pearson}} < 0.75$ ). The selected variables were (in the order of their relative contribution to the Maxent model): Precipitation of the driest month, isothermality, precipitation of the warmest quarter and maximum temperature of the warmest month. These variables are believed to directly influence ant distributions because many features of ant biology are sensitive to small differences in temperature [16] or humidity, for example foraging [11], oviposition rates [44], survival [10], the structure of foraging networks [12].

Future climatic data were sourced from the 4<sup>th</sup> IPCC assessment report [47]. The direct output of Global Climate Models is provided in the form of very large (500 km) grid cells because of the heavy calculations needed for the simulation of geophysical processes. To get a better resolution required for species distribution modelling, climate centres use statistical models to infer climatic variation at a more local scale, "downscaling" the data by using the WorldClim data for 'current' conditions for calibration. Therefore the projections at different time horizons can be compared. In order to consider a range of possible future climates, we used downscaled climate data from three Global Circulation Models (GCMs), provided by different climate centres, each based on different geophysical assumptions: the CCCMA-GCM2 model; the CSIRO-MK2 model; and the HCCPR-HADCM3 model [47]. We also used two extreme Special Report on CO<sub>2</sub> Emission Scenarios (SRES): the optimistic B2a and pessimistic A2a scenarios. In total, we used six future climatic scenarios (3 GCM×2 SRES). Data for the future climatic projections were climate data averaged across a decade, centred on the focal year (e.g. 2020) [47].

Worldclim data is the standard source of climate data for species distribution models. However it is poor at interpolating climate in topographically complex regions such as mountains or coastal regions [48]. But the focus of our study is projections at the global scale with a spatial resolution of 10 arcmin (approx. 18.5×18.5 km pixel), where complex coastlines are not visible. Predictions based on coarser resolutions are more likely to be controlled by climatic predictors, whereas fine-scale, patchy distributions at a smaller scale are more likely to be determined by micro-topographic variations or habitat fragmentation [49].

### Species Distribution Modelling

In order to make spatial predictions of potential distribution, we used species distribution models (SDMs), which explain the species' current distribution based on a set of climatic predictor variables. It has been shown that model outputs are sensitive to the algorithms, climatic data from different global climate models and different human development scenarios [50]. One way to deal with these uncertainties in species distribution modelling is to conduct a consensus forecast which can be defined as combining multiple simulations across a range of possible initial conditions and different classes of models [51].

To generate the consensus forecasts we used five machine learning methods, which are a set of algorithms that learn the mapping function or classification rule inductively from the input data [52]. The first two models were based on one- and two-class Support Vector Machines (SVMs) [39,31]. Two-class SVMs (SVM2) seek to find a hyperplane that maximally separates the two target classes. Recently, one-class SVMs have also been developed [42] that distinguish one specific category from all other categories. Third, we used Artificial Neural Networks (ANN), which extract linear combinations of the input variables as derived features (synthetic variables), and model the output as a nonlinear

function of these derived features [42,54]. Fourth, we used Classification Trees (CT), which partition the response variable into increasingly pure binary subsets with splits and stop criteria [41,42,53]. Finally we used the Maximum Entropy Method (Maxent) which estimates a probability distribution of a species being present by seeking the most widespread distribution, given a set of constraints [18,57,58]. For a more detailed description of these algorithms see [16,19]. All models were run using the ModEco Platform with default parameters [59].

A clear limitation of modelling is that outputs are dependent on the specifically chosen input settings, in this instance the algorithms, global climate models and scenarios of human development. To minimise potential resulting variation, we conducted consensus forecasts [51] using the outputs of the five different modelling techniques detailed above with each of three climate models (GCMs) and two CO<sub>2</sub> emission scenarios (SRES). The purpose of consensus forecasts is to separate the signal from the “noise” associated with the errors and uncertainties of individual models, by superposing the maps based on individual model outputs. Areas where these individual maps overlap are defined as areas of “consensual prediction” [51]. This is different from averaging the individual projections, as the area predicted by the consensus forecast can be smaller than any individual forecast if there is little spatial agreement (*i.e.*, overlap) between individual forecasts. Simple averaging across individual forecasts is considered unlikely to match reality [51].

The contribution of the individual models (*i.e.* the spatial prediction of “suitable range”) was weighted according to their AUC (section on model validation) in order to enhance contribution of models with higher model performance values (see [18]). Only binary projections (present or absent) have been combined to generate the consensus model because continuous outputs can have different meanings for different models and cannot be simply added together [59]. The combination of the individual forecasts then yields a projection (the consensus model), where the value of pixels vary between 0 and 1 and can be interpreted as a probability of the species occurring in each pixel [51].

The consensus model was generated using all 30 individual projections, each based on a different combination of CO<sub>2</sub> scenario × GCM × modelling technique, yielding a consensus projection for 4 time horizons (current, 2020, 2050 and 2080). The future climatic projections that we used as a basis of our models are in fact averaged climate data across a decade, centred on the focal year (*e.g.* 2020) [47].

### Model Validation

Model robustness was evaluated using the AUC of the ROC curve, which is a nonparametric threshold-independent measure of accuracy commonly used to evaluate species distribution models (*e.g.*, [18,60]). We used the AUC because it does not depend on the selected classification threshold, and it readily indicates if a model discriminates correctly between presence and absence points [18,60]. AUC values range from 0 to 1, where a value of 0.5 can be interpreted as a random prediction. AUC between 0.5 and 0.7 are considered low (poor model performance), 0.7–0.9 moderate and >0.9 high ([42] and references therein). For model evaluation, the data needs to be split into a train and a test group. Here, we used 10-fold cross-validation, whereby the data was split into 10 equal parts, with 9/10 of the observations used to build the models and the remaining 1/10 used to estimate performance. Validation was repeated ten times and the estimated performance measures were averaged [42,61].

### Assessing Climatically Suitable Areas

Studies with *a priori* objectives may use a range of different threshold values [62] to determine habitat suitability. As this was not the case here, we applied a limit whereby pixels with a probability of presence exceeding 0.5 were classified as “suitable” area, as is frequently done for binary classification for species distribution modelling [42,63]. Users of our models may want to minimize the chance of either over- or under-prediction of potential distribution (omission or commission errors) and to apply a different threshold. For example, for management decisions it could be better to apply a more “prudent” (lower) threshold that lowers the probability of omission errors. To allow these user-specific applications of our models, we provide maps with a continuous output with a probability of presence between 0 and 1 (with 0.1 intervals).

In addition, we created a difference map (future suitability map – current suitability map), which showed relative differences that are independent of any classification threshold and indicated areas where the climatic suitability improved or decreased. Second, we generated a “shift” map where we mapped the net gains, losses and stable ranges under current and future climatic conditions. Third, we calculated two indices that have been recently proposed as complementary measures to evaluate the extent of spatial shift [64]: the spatial congruence index ( $2a/2a+b+c$ ), based on the Sorensen-Dice dissimilarity measure, and the stable range ( $a/(a+b)$ ), which is a measure of spatial shift vs stability, whereby  $a$  = area suitable currently and in the future,  $b$  = area suitable currently only, and  $c$  = area suitable in the future only. Spatial analyses were carried out using DIVA-GIS [65] and Arcgis v. 9.3.

### Results

The AUC values indicated excellent model performance for all five algorithms in predicting the species’ distribution based on the consensus model (AUC values: SVM1 = 0.968, SVM2 = 0.991, Maxent = 0.998, ANN = 0.991, CT = 0.997).

#### Current Climatic Conditions

Maps of the consensus model under current and future climatic conditions by 2020, 2050 and 2080 indicated large and increasing suitable areas for *P. chinensis* (Fig. 1a–d). Under current climatic conditions, 3.33% of global landmass was predicted to be suitable for *P. chinensis*. The suitable range was unequally distributed among biogeographic regions, with the highest relative amount of suitable landmass found in North America (45%), followed by Asia (38%), South America (11%), Europe (3%) and Oceania (2%) (Fig. 2a). The relative proportion of suitable landmass was also highest in North America (Fig. 2b).

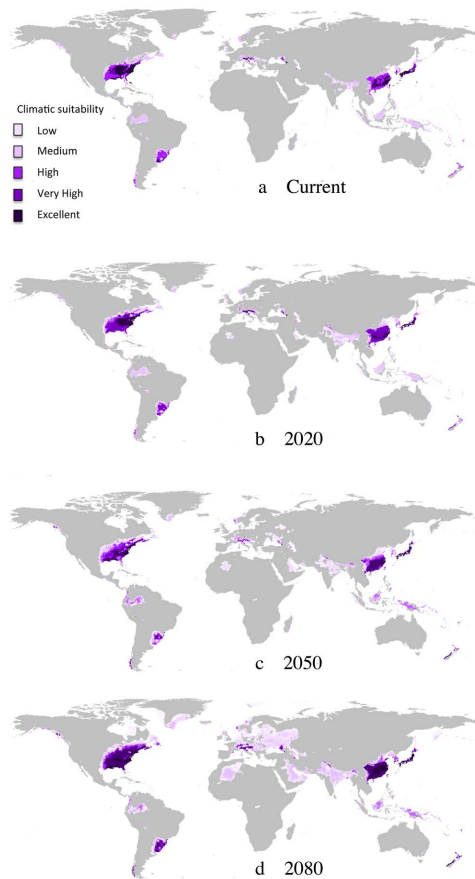
#### Climate Change Impacts

The suitable range for *P. chinensis* increased dramatically with projected climate change. In 2020 the potential range increased by 15.6%, in 2050 by 29.3% and in 2080 this increase reached +64.9% of the currently suitable landmass (Fig. 3).

By 2080, changes in suitable landmass differed greatly among biogeographic regions, with large increases in Europe (+210.1%, *i.e.*, +363,117 km<sup>2</sup>), Oceania (+75.1%, *i.e.*, +94,332 km<sup>2</sup>), North America (+74.9%, *i.e.*, +1,972,781 km<sup>2</sup>) and Asia (+62.7%, *i.e.*, +1,403,693 km<sup>2</sup>) and a decrease in Africa (–22.9%, *i.e.*, –2,042 km<sup>2</sup>).

#### Spatial Shifts of Suitable Conditions

The net changes in suitable landmass were almost exclusively due to gains in potential distribution (+4,350,682 km<sup>2</sup>, Fig. 4a).



**Figure 1. Maps of potential distribution.** Climatic suitability ranges from “low” (light purple) to “excellent” (dark purple). (a) Current climatic conditions (b) Consensus model of 6 future climatic scenarios (3 GCM×2 SRES) for 2020, (c) 2050 and (d) 2080. doi:10.1371/journal.pone.0075438.g001

Very small areas of suitable landmass was lost (i.e., suitable under current but not under future climatic conditions:  $-88,300 \text{ km}^2$ , Fig. 4a). These increases were from range expansions at the edge of the suitable range, but also entirely of new areas that became suitable (e.g. Europe, Northern Brazil or Indonesia, Fig. 4a). The stable range index was 0.569, meaning that only 56.9% of *P. chinensis*’ current potential range will remain suitable in the future. Spatial congruence was 0.722, which provides a measure of the stability (stable range) vs shift (losses and gains), indicating that 72.2% of all current and future suitable areas can be considered as “stable range” over time, whereas 27.8% will be either suitable currently or in the future, but not under both climatic scenarios.

The relative differences between the current and future areas of suitability, indicated that *P. chinensis* was likely to experience higher relative climatic suitability in all biogeographic regions, including large parts of north Africa, Arabia, India, South East Asia, north east America and eastern Europe (Fig. 4b). Few areas, such as the eastern USA showed a slight decrease of suitability (areas in light blue, Fig. 4b).

## Discussion

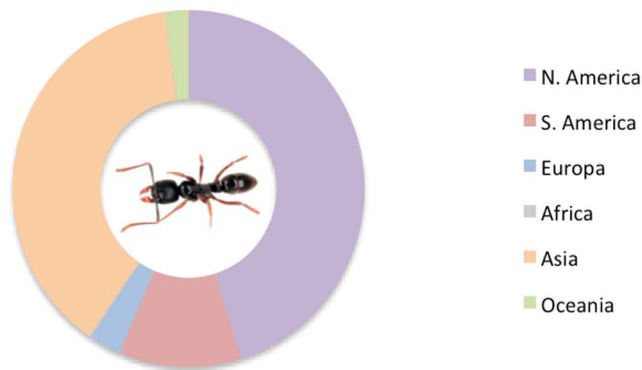
The Asian needle ant is native to Asia and has already invaded the South Eastern part of the USA [35]. Our models suggest that the species has a far greater invasive potential and is capable of

invading large parts of the global landmass on several continents, particularly north east America, South East Asia and south east America. In addition the consensus models suggest that climate change will exacerbate the risk of invasion by *P. chinensis* globally. Strikingly, the global suitable landmass is predicted to increase by 64.9% with climate change. At the regional scale, most of *P. chinensis*’ potential distribution was found in its Asian native range and in North America where the species is now considered invasive [35]. With climate change, the amount of suitable area for *P. chinensis* is predicted to greatly increase based on more suitable conditions, by 74.9% in North America. In addition, our models also predict a potential expansion into new biogeographic regions that should become suitable by 2080, in particular Europe, South America or Indonesia and an expansion in Asia relative to its current known distribution range.

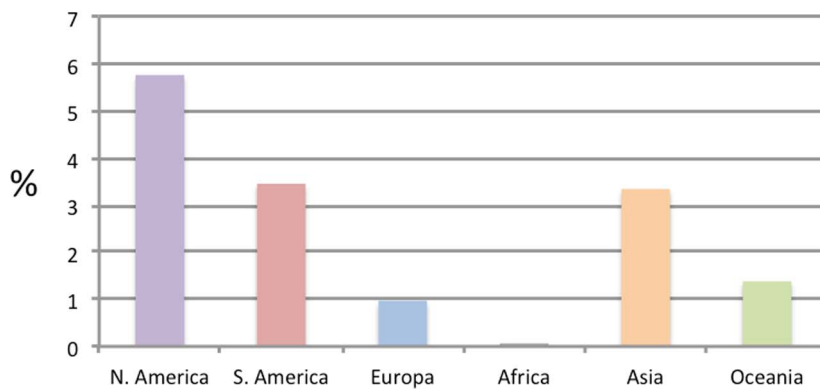
In addition to direct climatic suitability, climate change could enhance the invasion likelihood by disadvantaging other competing ants in the invaded areas. Ant community structures are known to be temperature-dependent [13,66], and therefore a change in temperature might lead to new invaders dominating. For example, *P. chinensis* has recently been found to establish in sites dominated by the invasive Argentine ant, *L. humile*, resulting in a dominance swap and even localised extinction of *L. humile* [65]. Because *P. chinensis* does not seem to be behaviourally dominant, this dominance shift has been attributed to differences in the climatic preferences of the two species, with *P. chinensis* establishing nests and expanding its population earlier in the season when temperatures were lower before *L. humile* populations could expand [65].

Our consensus models for the potential distribution had a high accuracy (good to excellent AUC) and were designed to include a broad range of climate change scenarios, with an optimistic B2a and a pessimistic A2a CO<sub>2</sub> emission scenario and three global circulation climatic models [47]. We additionally reduced uncertainty due to single modelling methods by building models with five different algorithms that contributed to the final consensus forecast [51]. Nevertheless, inherent uncertainty in the spatial projection remains because of the underlying assumptions shared by all species distributions models [49], [46] in that they assume that the species is in equilibrium with its environment and therefore its current distribution reflects the ideal climatic conditions for the species, which can be used to model its potential distribution. That means that a model of the potential distribution of an invasive species with climate change has to make two extrapolations: 1) in space (invasion of a different place); and 2) in time (with future climate change). However, niche shifts during invasions are possible and have already been observed [67–69] and species may display phenotypic plasticity or show evolutionary adaptations, such as has been shown for the Asian ladybeetle which has the same invasion pattern as *P. chinensis*, dispersing from Asia to the east coast of North America [70]. Therefore, projections for invasions under climate change come necessarily with some uncertainty and should be only viewed as an attempt to evaluate future trends and invasion risks, and not as a precise prediction at a small scale. For example, a new occurrence point of *P. chinensis* has been recently recorded in Washington D.C. by the School of Ants project [71], where the species does not find ‘excellent’ climatic conditions according to our projections. One of the inherent problems of species distribution models is that the species may be able to occur within areas predicted to be of relatively low suitability, if the microclimatic conditions favour the species or if it is associated to human infrastructure. Despite these limitations, species distribution

## Distribution of favourable landmass (a)



## Proportion of suitable landmass (b)

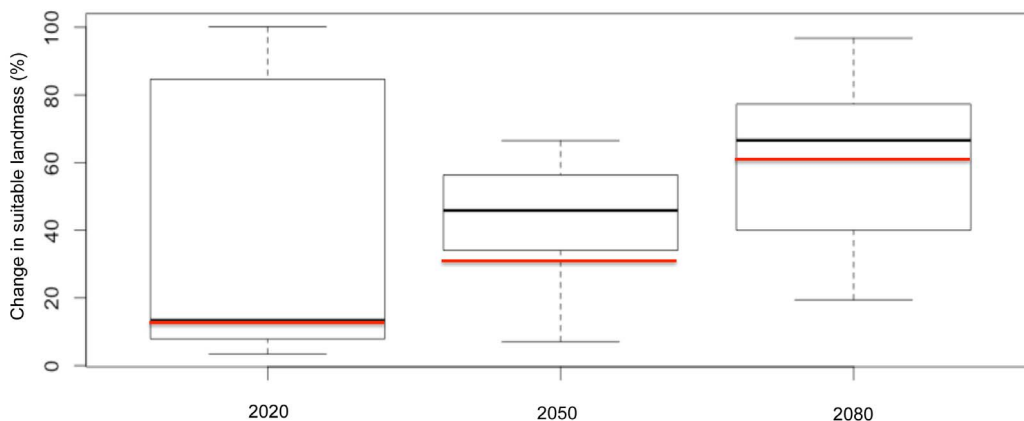


**Figure 2. a+b Distribution and proportion of suitable landmass under current climatic conditions among six biogeographic regions.**

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models are generally considered to deliver useful approximations [72,73].

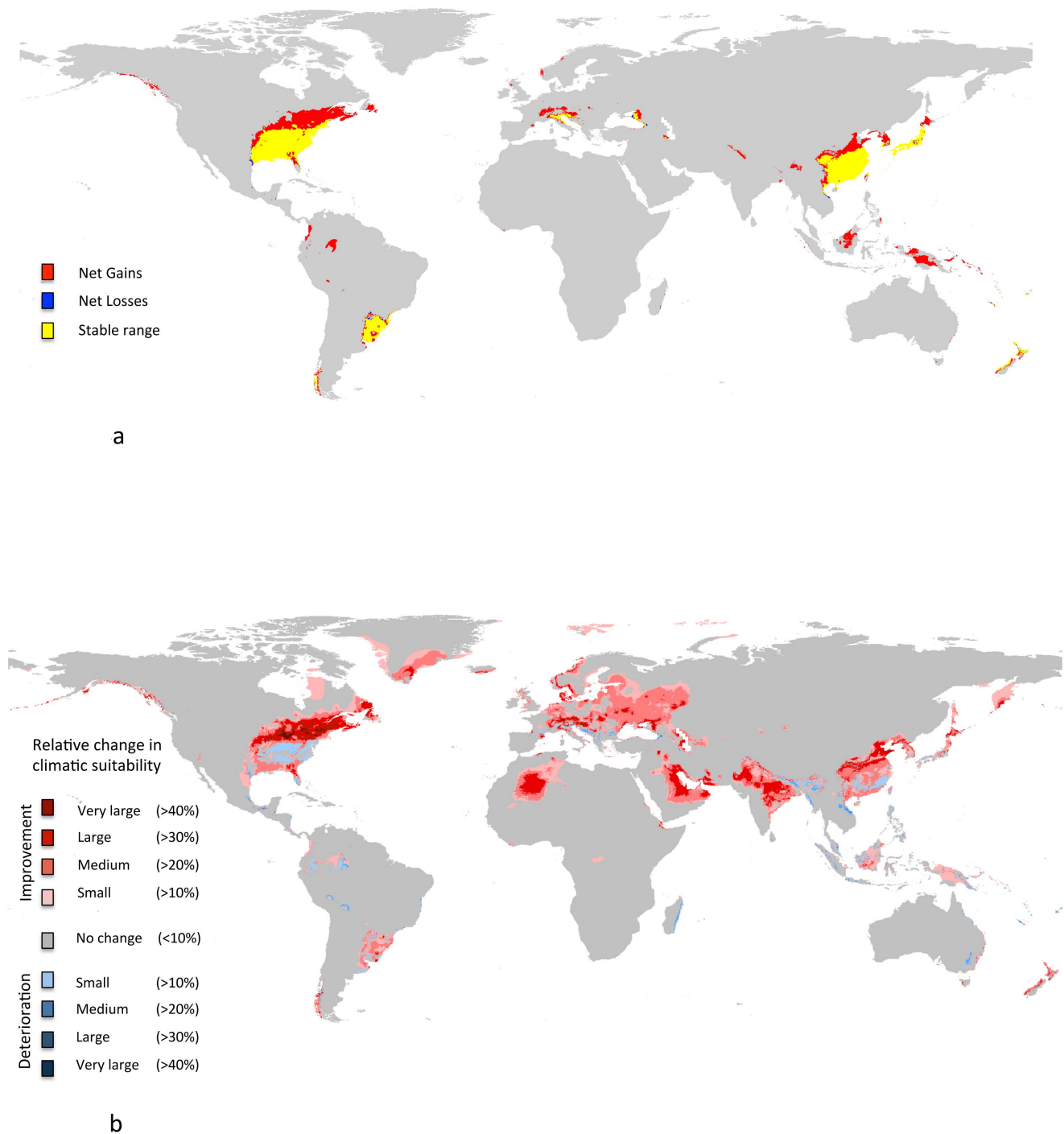
A further factor to consider is that numerous native species are predicted to suffer the effects from climate change [26]. This may



**Figure 3. Change in suitable landmass over time relative to the currently suitable landmass.** The boxplot represents variation of projections across six future climatic scenarios, each based on a different combination of Global Climate Model  $\times$  CO<sub>2</sub> emission scenario, per time horizon ( $\pm$  s.d). The red line indicates the value of the consensus model.

doi:10.1371/journal.pone.0075438.g003





**Figure 4. Differences in suitable climatic conditions between the current climate and the consensus projection in 2080.** (a) Net gains (red), losses (blue) and stable range (yellow), (b) Relative differences in suitability: red colors indicate improved climatic suitability (light to dark red gradient indicates the relative change in suitability), blue colors indicate deteriorated climatic suitability for *P. chinensis*. doi:10.1371/journal.pone.0075438.g004

increase the vulnerability of the community by decreasing the biotic resistance to new invaders [74,75]. This could even further exacerbate the invasion risk of *P. chinensis*.

Our study solely focused on the role of climate change on the potential distribution of a newly invasive ant species because climate has been shown to be very important in determining the distribution of ants at a global scale [22–24] as well as being the most important factor influencing the global invasion of the

Argentine ant [25]. Therefore, climate is probably a crucial factor limiting the distribution of other invasive ants, such as *P. chinensis*. For future studies, predictions of invasive potential will be advanced by investigations into the influence of other abiotic factors and drivers of species displacement. At a finer scale for example, topographic or terrain variables, such as elevation, geomorphology or hydrology can be important [42]. For example, appropriate soil moisture levels can be an important requirement

for nest location of ants. Also important is the effect of disturbance regimes, because invasive ants are frequently associated with disturbed habitats [76,77]. However, it should be noted that *P. chinensis* has been found to invade intact forests [36].

Our results support the view that biological invasions could increase due to climate change [60,61,62,10,11] and show it can do so dramatically. In this way two of the most important threats to global biodiversity (invasive species and climate change) may interact synergistically. An important observation is that the potential distribution of *P. chinensis* exists at a wide range of latitudes, and thus this species' potential range did not simply shift to higher latitudes. Consequently, invasion risk was exacerbated globally with entirely new areas covering large amounts of landmass becoming suitable. Given the important ecological impacts of *P. chinensis* [35] and its ability to potentially even displace one of the most aggressive and dominant species of invasive ants, the *L. humile* [81], clearly it is important that surveillance efforts of this species are increased to prevent further spread and aid early detection. Eradication of well established large invasive ant populations can be extremely challenging [32] if not impossible, but early detection of small incipient populations can enable managers to carry out early responses and achieve eradication [34]. The use of species distribution models to inform risk assessments is increasingly becoming standard, but a spatial

model should be always viewed in the light of the many uncertainties associated with the approach [58]. Species distribution models can serve as a guide to prioritize surveillance efforts in certain regions. Ideally, this approach should be complemented with interception data at ports of entry. The results of our study suggest *P. chinensis* deserves increased attention in new regions of the world (e.g., Europe and South America) as a rising exotic species of significance.

## Supporting Information

**Figure S1 Occurrence points of *P. chinensis***  
(TIF)

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## Author Contributions

Conceived and designed the experiments: CB FC BG. Performed the experiments: CB. Analyzed the data: CB FC. Contributed reagents/materials/analysis tools: CB GB FC. Wrote the paper: CB FC GB.

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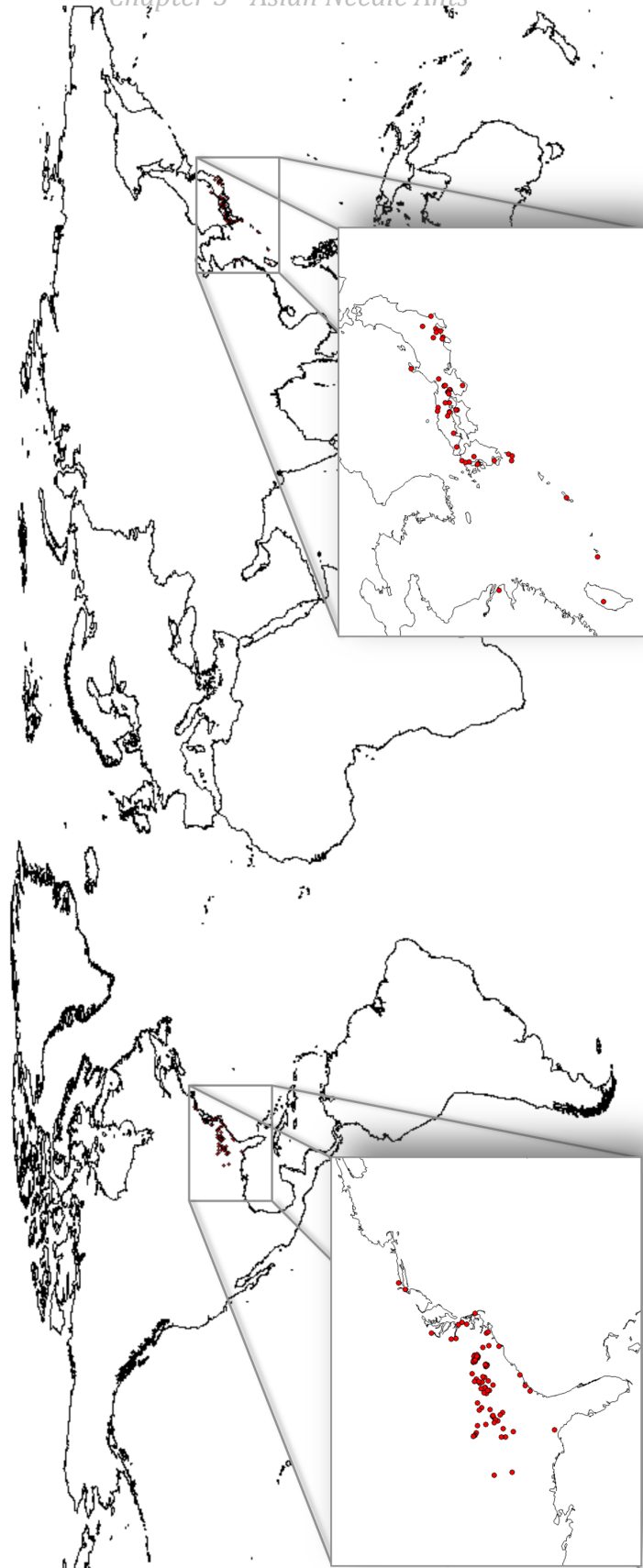


Fig. S1



# Increase in Quantity and Quality of Suitable Areas for Invasive Species as Climate Changes

Cleo Bertelsmeier, Gloria M. Luque and Franck Courchamp





# Increase in Quantity and Quality of Suitable Areas for Invasive Species as Climate Changes

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**Abstract:** As climatically suitable range projections become increasingly used to assess distributions of species, we recommend systematic assessments of the quality of habitat in addition to the classical binary classification of habitat. We devised a method to assess occurrence probability, captured by a climatic suitability index, through which we could determine variations in the quality of potential habitat. This relative risk assessment circumvents the use of an arbitrary suitability threshold. We illustrated our method with 2 case studies on invasive ant species. We estimated invasion potential of the destroyer ant (*Monomorium destructor*) and the European fire ant (*Myrmica rubra*) on a global scale currently and by 2080 with climate change. We found that 21.1% of the world's landmass currently has a suitable climate for the destroyer ant and 16% has a suitable climate for European fire ant. Our climatic suitability index showed that both ant species would benefit from climate change, but in different ways. The size of the potential distribution increased by 35.8% for the destroyer ant. Meanwhile, the total area of potential distribution remained the same for the European fire ant (>0.05%), but the level of climatic suitability within this range increased greatly and led to an improvement in habitat quality (i.e., of invasive species' establishment likelihood). Either through quantity or quality of suitable areas, both invasive ant species are likely to increase the extent of their invasion in the future, following global climate change. Our results show that species may increase their range if either more areas become suitable or if the available areas present improved suitability. Studies in which an arbitrary suitability threshold was used may overlook changes in area quality within climatically suitable areas and as a result reach incorrect predictions.

**Keywords:** biological invasions, climate change, consensus model, *Monomorium destructor*, *Myrmica rubra*, niche modeling

Incremento de la Cantidad y Calidad de Áreas Idóneas para Especies Invasoras a Medida que Cambia el Clima

**Resumen:** A medida que incrementa el uso de proyecciones de rangos adecuados climáticamente para evaluar la distribución de especies, recomendamos evaluaciones sistemáticas de la calidad del hábitat adicionalmente a la clasificación binaria del hábitat. Diseñamos un método para evaluar la probabilidad de ocurrencia, capturada por un índice de idoneidad climática, mediante el cual pudimos determinar variaciones en la calidad de hábitat potencial. Esta evaluación de riesgo relativo evita el uso de un umbral de idoneidad arbitrario. Ilustramos nuestro método con 2 casos de estudio de especies de hormigas invasoras. Estimamos el potencial de invasión de *Monomorium destructor* y de *Myrmica rubra* a escala global actualmente y en 2080 con cambio climático. Encontramos que 21.1% de las tierras emergidas del mundo tiene un clima adecuado para *M. destructor* y 16% tiene clima adecuado para *M. rubra*. Nuestro índice de idoneidad climática mostró que ambas especies de hormigas se beneficiarían del cambio climático, pero de manera diferente. El tamaño de la distribución potencial incrementó en 35.8% para *M. destructor*. Mientras que el área total de distribución potencial de *M. rubra* permaneció igual (>0.05%), pero el nivel de idoneidad climática en este rango incrementó mucho y llevó a un mejoramiento de la calidad del hábitat (i.e., la probabilidad de establecimiento de una especie invasora). Ya sea mediante la cantidad o calidad de áreas idóneas, es probable que ambas especies de hormigas invasoras incrementen la extensión de su invasión en el futuro, siguiendo al cambio climático global. Nuestros resultados muestran que las especies pueden incrementar su rango tanto si más áreas se vuelven idóneas o si las áreas disponibles presentan mejor

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*idoneidad. Estudios que utilicen un umbral de idoneidad arbitrario pueden soslayar cambios en la calidad del área en áreas idóneas climáticamente y como resultado pueden llegar a predicciones incorrectas.*

**Palabras Clave:** cambio climático, invasiones biológicas, modelado de nicho, modelo de consenso, *Monomorium destructor*, *Myrmica rubra*

## Introduction

Bioclimatic niche models have been used in various fields of conservation biology particularly to predict the potential dynamics of biological invasions, to discover previously unknown species, to map risks of disease transmission, and to forecast the effects of climate change or land-use changes on the future of biodiversity (Sinclair et al. 2010; Araújo & Peterson 2012; Bellard et al. 2012). Conservation biologists of the 21st century will face a number of critical decisions regarding assisted colonization (Hewitt et al. 2011), triage-based assessments (Bottrill et al. 2008), and prioritization of protected areas (Summers et al. 2012). Some of these decisions will be based on bioclimatic models. Thus, it is important to correctly assess the effect of climate change on the distribution of species, be they threatened or invasive.

We highlight a way in which classical assessments of potential range size can lead to misleading conclusions when projections are made, either spatially (e.g., for translocation-success or invasion-risk assessments) or temporally (e.g., accounting for climate change). Climatic niche models are frequently used to estimate the quantity of landmass climatically suitable for the focal species. This is achieved by establishing distribution maps of areas that are above a given suitability threshold for a combination of climatic parameters of relevance for the species (e.g., Bakkenes et al. 2002; Thomas et al. 2004; Cheaib et al. 2012). Most applications of niche models require such binary predictions of presence-absence maps for the focal species (Franklin 2009). Among the numerous possible applications, for example, binary quantification of areas as either suitable or unsuitable can be used in conjunction with species-area relations to determine the threatened status of a species in the future (Thomas et al. 2004). Binary predictions are also frequently used to evaluate invasion risk of a particular species (e.g., Bertelsmeier et al. 2013) or region (O'Donnell et al. 2011).

However, the choice of the threshold used to transform a probability of presence into a binary prediction is one of the least explored sources of uncertainty in climatic niche modeling, and no guidelines for threshold selection exist (Nenzén & Araújo 2011). The choice of classification thresholds is the second-most important factor affecting uncertainty in projections. The most important factor is choice of modeling method. Different thresholds produced up to 10-fold differences in the proportions of species projected to become threatened by climate change (Nenzén & Araújo 2011). Despite the

great variability in projections due to the choice of different thresholds, Nenzén and Araújo (2011) highlight that the question of the choice of the most suitable threshold remains unanswered. Yet, regardless of the chosen threshold a binary classification of suitable versus unsuitable areas always leads to a loss of information. Indeed, niche models usually provide an occurrence probability (or similar) for each pixel as output, which is then classically transformed into “unsuitable” below a given probability threshold and “suitable” above. Several pioneer studies were conducted to make more informative use of these model outputs. For example, Normand et al. (2009) used the shape of the probability distribution to infer the importance of abiotic stresses at different elevations and latitudes. Keith et al. (2008) converted the net value of the probability of occurrence into a carrying capacity of a given pixel, thereby allowing one to link climatic niche models and stochastic population models. Although more informative, this approach needs data on population dynamics, which is not available for many species. Therefore, it cannot replace classical distribution modeling that requires only occurrence data. However, the use of the output of niche models needs to be improved.

We devised a method to circumvent binary classification. We propose that binary classification would be advantageously replaced by an assessment of the qualitative climatic suitability (CS) that would take into account different levels of CS. Moreover, a CS index could be used to summarize the range of possible levels of CS as an overall mean suitability. This additional information regarding CS is essential because climatically suitable ranges can evolve not only in quantity but also in quality, a point that cannot be accounted for with the use of a suitability threshold.

We applied our approach to 2 highly invasive species of the same family, the Formicidae: the destroyer ant (*Monomorium destructor*) and the European fire ant (*Myrmica rubra*). Classically, we inferred the size of the potential distribution through a binary classification of the climatically suitable areas. In addition, we assessed the level of CS within these favorable areas, with an index of suitability. We based this index on a spatial prediction of different probabilities of establishment, ranging from low to excellent suitability of the area. With this more complete approach, we characterized the current potential distribution worldwide for the 2 ant species and how it is distributed among 6 broad geographic regions; characterized the change in this potential distribution by 2080 following global climate change; compared

these changes among North America, South America, Europe, Africa, Asia, and Oceania. For each of these points, changes in CS have been assessed qualitatively and quantitatively, eventually demonstrating that making both types of assessment can be crucial for evaluating future invasion risks.

## Methods

### Case Study

Destroyer ants and European fire ants are of high interest to biodiversity managers because they are listed among the world's most problematic invasive species (IUCN 2012) due to the extent of their negative social, economic, and environmental effects (Grodén et al. 2005; Harris et al. 2005; von Aesch & Cherix 2005). The extent of their potential area of invasion has not been studied.

The destroyer ant is believed to be native to India (von Aesch & Cherix 2005) and most frequently invades disturbed and semiarid areas in the tropics and subtropics (Wetterer 2009). The species can displace native invertebrate fauna through aggression and is a great nuisance to humans because they can damage electrical equipment (cars, televisions, telecommunication equipment) and may carry disease (Harris et al. 2005).

The European fire ant is common in deciduous woodlands, gardens, and grasslands throughout Eurasia (Fokuhl et al. 2007) and has been introduced to North America, where it reaches high nest densities (Grodén et al. 2005). The species can decrease invertebrate richness and inflicts very painful stings on humans and livestock (Harris et al. 2005).

### Species Distribution Data

Ecological niche models are used to detect nonrandom associations between environmental predictors and species occurrence data on which predictions of potential spatial distribution can be made. Because our models should include the full set of climatic conditions under which the target species can exist, we included occurrence points (presence-only data) from invaded and native areas (Beaumont et al. 2009). The data were sourced from the International Union for the Conservation of Nature globally authoritative database of invasive species (IUCN 2012) and a database of ant distributions (Harris & Rees 2004). We obtained additional points for the destroyer ant from Wetterer (2009). Data were excluded where the species were present in artificial climatic conditions, such as greenhouses, or were collected prior to the second half of the 20th century. We used 116 occurrence points for *M. destructor* and 123 for *M. rubra* (Supporting Information). For models requiring absence

data, 10,000 pseudo-absence (background) points were generated randomly from all around the world to provide background data. This is a classic procedure because confirmed absence data are difficult to obtain for most species and requires great sampling efforts (Franklin 2009).

### Climatic Predictors

We modeled species niche on the basis of 6 of the 19 bioclimatic variables provided by the Worldclim database (Hijmans et al. 2005) that were not collinear (pairwise  $r_{\text{Pearson}} < 0.75$ ) (Supporting Information). These bioclimatic variables are derived from monthly temperature and rainfall values from 1960 to 1990 (Hijmans et al. 2005) and affect species distributions (Root et al. 2003).

We sourced future climatic data from the 4th Intergovernmental Panel on Climate Change (IPCC) assessment report (GIEC 2007). The data set provided by the IPCC consisted of projections that had been calibrated and statistically downscaled with the WorldClim data for current conditions; therefore, the projections can be compared. To consider a range of possible future climates, we used downscaled climate data from 3 global circulation models (GCMs): CCCMA-GCM2 model, CSIRO-MK2 model, and HCCPR-HADCM3 model (GIEC 2007). Similarly, we used the 2 extreme Special Report on CO<sub>2</sub> Emission Scenarios (SRES): the optimistic B2a and pessimistic A2a scenarios. We used a spatial resolution of 10 arcmin (approximately 18.5 × 18.5 km pixel) because our aim was to make global projections. Predictions made on the basis of coarser resolutions are more likely to be controlled by climatic predictors, whereas fine-scale, patchy distributions at a smaller scale are more likely to be determined by microtopographic variations or habitat fragmentation (Guisan & Thuiller 2005).

### Ecological Niche Modeling

We used 5 machine-learning modeling techniques to generate the consensus forecasts. Machine-learning methods are a set of algorithms that learn the mapping function or classification rule inductively from the input data (Elith et al. 2006).

We based the first 2 models on support vector machines (SVM), which are a new generation of learning algorithms (Cristianini & Schölkopf 2002) and are considered a promising new approach in niche modeling (Guo et al. 2005). Ordinarily, SVMs are algorithms used for 2-class problems that thus require both presence and absence data. For these classification problems, 2-class SVMs find a hyperplane in the feature space that maximally separates the 2 target classes. Recently, 1-class SVMs have also been developed (Franklin 2009). They distinguish one specific category from all other categories. Thus, we used 1-class SVMs (parameters: kernel = radial

base function) and 2-class SVMs (parameters: kernel = radial base function, cost = 1).

We used artificial neural networks (ANN) (parameters: type = back propagation ANN, momentum = 0.3, learning rate = 0.1) to model the complex relations between dependent variables and independent variables. ANN extract linear combinations of the input variables as derived features (synthetic variables) and model the output as a nonlinear function of these derived features (Hastie et al. 2001). ANN have been used successfully to predict species distribution (Maravelias et al. 2003; Franklin 2009).

We also used classification trees (CT) (parameters: type = iterative, window size = 10, pruning level = 0.25), which partition the response variable into increasingly pure binary subsets with splits and stop criteria (De'ath & Fabricius 2000). Trees can overgrow to exactly fit the training data, but this form of over fitting can be avoided with pruning rules that identify the most parsimonious combination of predictor variables. CT can detect hierarchical and nonlinear relations among predictor variables (De'ath & Fabricius 2000) and have been applied to species-distribution modeling in the light of global changes (e.g., Broennimann et al. 2006). The result of the CT was an average across 10 iterations of the model algorithm.

We used the maximum entropy method (Maxent) to estimate a probability distribution of a species being present. Maxent identifies the most spread out distribution, given a set of constraints. The constraints of the target distribution are determined by the set of climatic variables: the expected value of each variable should match its empirical average (i.e., the average value for a set of sample points) (Phillips et al. 2006). Maxent generally performs well and has been widely used for distribution models for invasive species and effects of climate change (Phillips et al. 2006; Roura-Pascual et al. 2009; Jimenez-Valverde et al. 2011). Pros and cons of all models are provided in Supporting Information. All models were run in the ModEco Platform with default parameters (Guo & Liu 2010).

A clear limitation of modeling is that outputs depend on the specifically chosen input settings, in this instance the algorithms, global climate models, and scenarios of human development. To minimize potential resulting variation, we conducted consensual forecasts (Araújo & New 2007) of combined models with the 5 different modeling techniques above with each of 3 climate models (GCMs) and 2 CO<sub>2</sub> emission scenarios. The purpose of consensual forecasts is to separate the signal from the noise associated with the errors and uncertainties of individual models by superposing the maps that are based on individual model outputs. Areas where these individual maps overlap are considered areas of consensual prediction (Araújo & New 2007). This consensus forecast is different from averaging the individual projections because the area pre-

dicted by the consensual forecast can be smaller than any individual forecast if there is little spatial agreement (i.e., overlap) between individual forecasts. Simple averaging across individual forecasts is considered unlikely to match the reality; therefore, ensemble averages or confidence limits for the consensual prediction are classically not calculated (Araújo & New 2007).

We weighted the contribution of the individual models (i.e., the spatial prediction of suitable climatic range) according to their area under the curve (AUC) of the receiver operating characteristic (ROC) curve (see Model Validation below) in order to enhance contribution of models with higher model-performance values (Roura-Pascual et al. 2009). The AUC of the ROC curve is a non-parametric threshold-independent measure of accuracy commonly used to evaluate species-distribution models (e.g., Pearce & Ferrier 2000; Roura-Pascual et al. 2009). Only binary projections (present or absent) have been combined to generate the consensus model because continuous outputs can have different meanings for different models and cannot be simply added together (Guo & Liu 2010). The combination of the individual forecasts then yields a projection (the consensus model), where the value of pixels vary between 0 and 1 and can be interpreted as a probability of the species being present in each pixel (Araújo & New 2007).

We generated the consensus model with all 30 individual projections, each was based on a different combination of CO<sub>2</sub> scenario × GCM × modeling technique, and each yielded a consensus projection for one particular point in time. Consequently, we obtained a single value per consensus model, which we illustrated in the form of histograms. But because the underlying idea of consensus models is to incorporate the variation, there cannot be error bars of the variation between single models in the figures.

### Model Validation

We evaluated model robustness with the AUC of the ROC curve because it does not depend on the selected classification threshold and readily indicates whether a model discriminates correctly between presence and absence points (Pearce & Ferrier 2000; Roura-Pascual et al. 2009). The AUC values range from 0 to 1, where a value of 0.5 can be interpreted as a random prediction. An AUC value between 0.5 and 0.7 is considered low (poor model performance), 0.7–0.9 moderate, and >0.9 high (Franklin 2009). For model evaluation, the data need to be split into a train and a test group. We used 10-fold cross-validation, whereby the data have been split into 10 equal parts, with 9/10 of the observations used to build the models and the remaining 1/10 used to estimate performance; this procedure was repeated 10 times and the estimated performance measures were averaged (Fielding & Bell 1997; Franklin 2009).

### Assessing Climatically Suitable Areas

Studies with a priori objectives may use a range of different threshold values (Nenzén & Araújo 2011). Because we did not have an a priori objective, we applied a limit whereby all pixels with a probability of presence exceeding 0.5 were classified as favorable areas, as is frequently done for binary classification for species-distribution modeling (Franklin 2009; Klamt et al. 2011). We used DIVA-GIS for spatial analyses (Hijmans et al. 2001).

To evaluate whether the quality of the available ranges changed, we divided the favorable range within the current and the future climatic model into 5 classes that ranged from low ( $0.5 < p < 0.6$ ) to excellent climate suitability ( $0.9 < p < 1$ ). Next, we compared the change of classes over time. We also calculated mean CS, which we refer to as the CS index. We used the following equation to calculate index values: the sum of the pixels of each category of suitable climate range weighted by the average probability of occurrence of each of the categories (0.55, 0.65, 0.75, 0.85, 0.95) divided by the total number of pixels within the suitable range:

$$CS = \frac{\sum_{i=1}^{i=c} n_i p_i}{N}, \quad (1)$$

where  $n_i$  is the number of pixels in each of the  $c$  quality categories (here 5),  $p_i$  is the weight of category  $i$  (i.e., average probability of occurrence of each category [(0.55, 0.65, 0.75, 0.85, 0.95) or its quality]), and  $N$  is the total number of pixels in the suitable climate range. The index ranged from 0.5 to 1 and can be interpreted as the mean probability of establishment within the favorable range. We used a Wilcoxon rank-sum test in R (version 2.12.2) to test for differences in CS following climate change.

## Results

All AUC values were between 0.793 and 0.977, indicating an overall good to excellent ability to predict the species' presence on the basis of consensus models (Supporting Information).

### Current Suitable Climatic Range

With the classical suitability threshold set at 0.5, a high proportion of global landmass was favorable under current climatic conditions for both species: 21.1% for *M. destructor* and 16% for *M. rubra*. The potential distribution of *M. destructor* was predominantly in the southern hemisphere, whereas a large proportion of the potential distribution of *M. rubra* was in the northern hemisphere (Fig. 1).

Current favorable climatic conditions for *M. destructor* covered 3.3% of the landmass of North America, 60.3% of

South America, 0.01% of Europe, 48.8% of Africa, 13.3% of Asia, and 25% of Oceania. Globally, Africa contributed the greatest area (39%), followed by South America (29%) and Asia (22.5%; Fig. 2a). For *M. rubra*, current climatically suitable area covered 11.4% of North America, 11.3% of South America, 79.7% of Europe, 4.8% of Africa, 7.3% of Asia, and 11.5% of Oceania. The relative contributions of regions varied from 49% of Europe to 3.6% of Oceania (Fig. 2b).

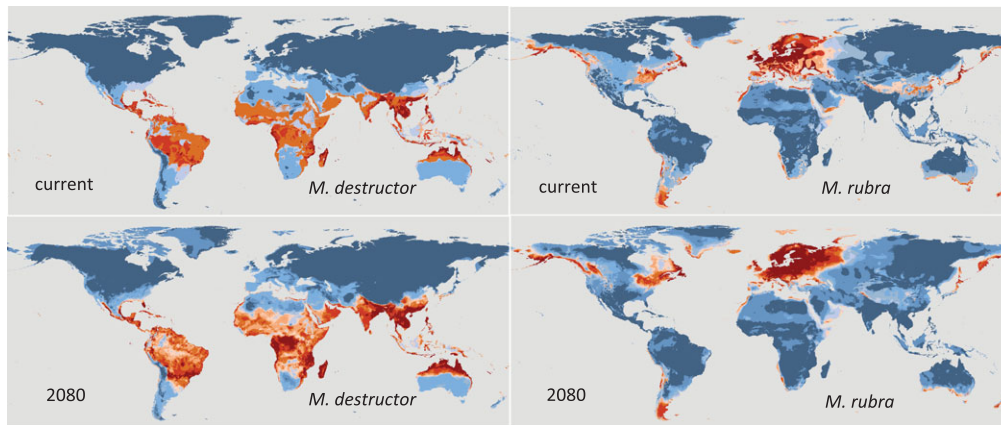
### Quantitative Changes Following Climate Change

Changes in suitable areas were markedly different for the 2 species, both globally and among regions (Fig. 1). For *M. destructor*, the 2080 projection of land area with suitable climate increased by 35.8% globally, contrasting with a negligible change of suitable area for *M. rubra* (0.05% increase). For *M. destructor*, the potential distribution increased 6,614,046 km<sup>2</sup> in Africa, 3,902,005 km<sup>2</sup> in Asia, 2,471,088 km<sup>2</sup> in South America, 1,116,955 km<sup>2</sup> in Oceania, 523,239 km<sup>2</sup> in North America, and 111,314 km<sup>2</sup> in Europe (Fig. 3a). For *M. rubra*, climatically suitable area increased only in North America (3,431,359 km<sup>2</sup> increase) and in Europe (1,524,109 km<sup>2</sup> increase) and decreased in Asia by 2,565,870 km<sup>2</sup>, in Africa by 533,266 km<sup>2</sup>, in South America by 475,509 km<sup>2</sup>, and in Oceania by 223,057 km<sup>2</sup> (Fig. 3b).

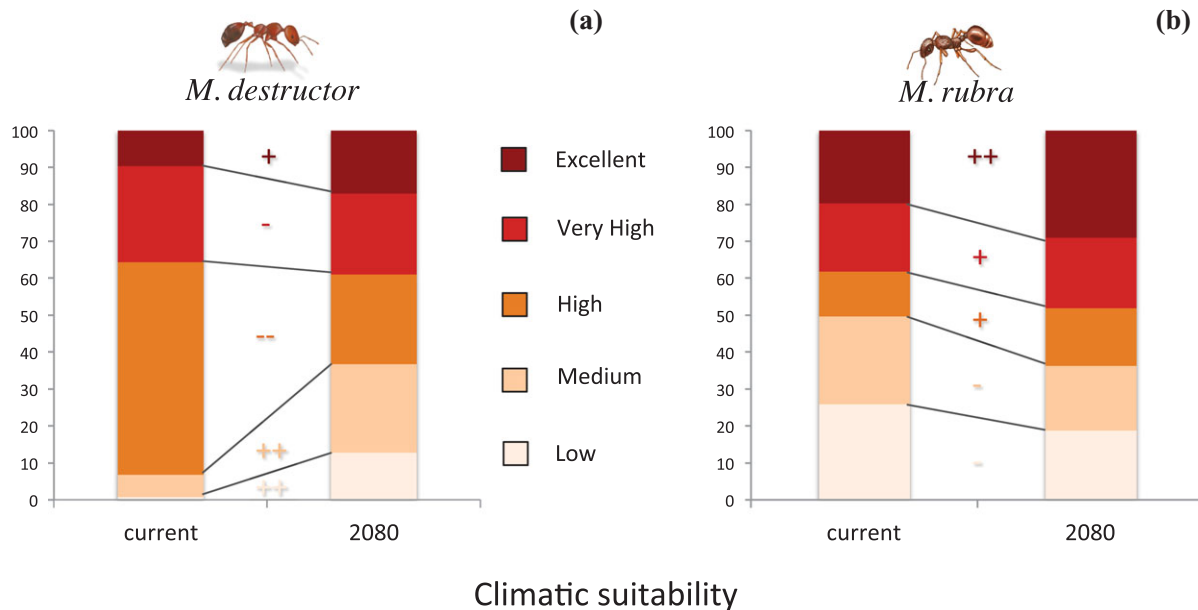
### Qualitative Changes Following Climate Change

Overall, the quantity of climatically favorable areas increased for *M. destructor*, whereas general CS decreased. The large increase in the amount of favorable area of *M. destructor* was mainly due to an increase of the lower categories of suitability (i.e., low from 0.8% of the favorable range to 12.8% and medium from 5.9% to 23.9%). In contrast, the relative increase in excellent CS was less pronounced (from 9.7% to 17%), and there was even a decrease in areas of high CS (from 57.6% to 24.3%) and very high (from 26% to 21.9%) suitability (Fig. 4a). In sum, the quantity of climatically favorable areas largely increased for the destroyer ant (Fig. 3a), but there was a general decrease of CS throughout this potential range even though the size of the range increased (Fig. 4a). Overall, CS index value of the favorable range of *M. destructor* decreased from 0.788 under current climatic conditions to 0.756 in 2080 (Wilcoxon rank-sum test,  $p < 0.001$ ). This index varied among regions, improving slightly in Oceania (from 0.82 to 0.828) and decreasing in the 5 other regions (Wilcoxon rank-sum test,  $p < 0.001$ ) (Fig. 5a).

The area of favorable range remained unchanged for *M. rubra*, but the probability of establishment increased from 0.732 under current climatic conditions to 0.772 in 2080. Indeed, the proportion of pixels presenting lower suitability decreased markedly (from 25.9% to 18.8% for



**Figure 1.** Results of consensus models of suitable climatic range for the invasive ants *M. destructor* and *M. rubra* under current climatic conditions and in 2080 (following global climate change) (reds, favorable areas from low climatic suitability [light rose, 0.5–0.6] to excellent climatic suitability [dark red, 0.9–1.0]; blues, unfavorable areas [dark, very unsuitable, probability of occurrence 0–0.1; light, slightly unsuitable, probability of occurrence 0.4–0.5]). The different color tones can be viewed as different degrees of suitability or, alternatively, as indicating the confidence of the model in predicting species presence or absence in a particular location.



**Figure 2.** Distribution of climatically suitable areas for (a) *M. destructor* and (b) *M. rubra* among the geographic regions under current and future climatic conditions.

low suitability and from 23.8% to 17.4% for medium suitability), whereas the areas with higher suitability increased (from 12.2% to 15.7% for high suitability, from 18.4% to 19.1% for very high suitability, and from 19.7% to 29% for excellent suitability) (Fig. 4b). The potential distribution increased in North America, South America, Europe, and Asia (Fig. 3b) and decreased in Africa and Oceania, which contributed a small proportion of suitable areas. The highest increase in CS was in Europe (increase from 0.791 to 0.841; Wilcoxon rank-sum test,  $p < 0.001$ ), and the lowest increase was in Asia (increase

from 0.656 to 0.681; Wilcoxon rank-sum test,  $p < 0.001$ ) (Fig. 5b).

## Discussion

Through bioclimatic models of the potential worldwide distribution of 2 invasive ants, we showed that global climate change was likely to benefit both invaders, one through an increase in the quantity of suitable areas and the other through an increase in the suitability in favorable areas.

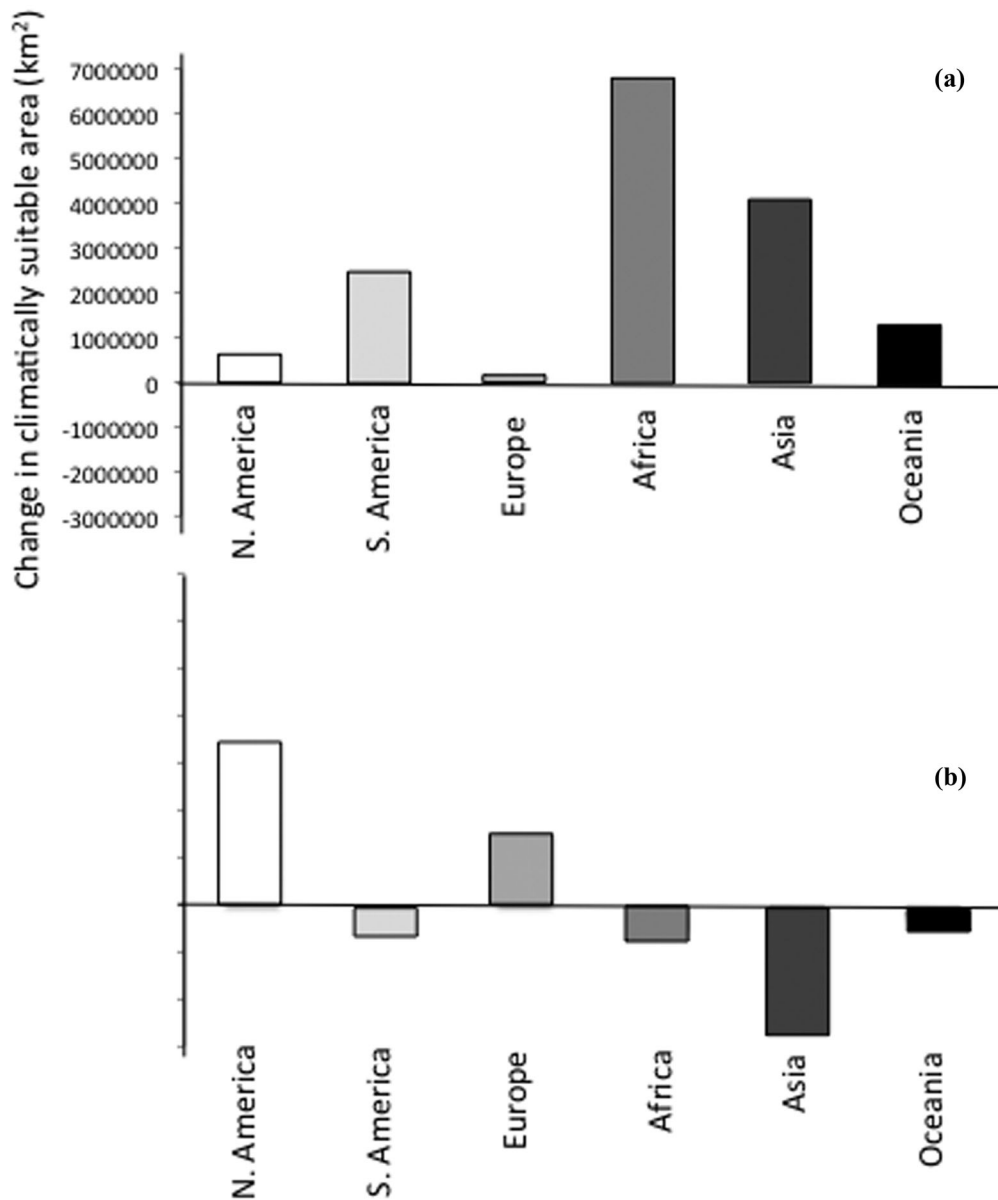


Figure 3. Changes in the amount of climatically suitable area for (a) *M. destructor* and (b) *M. rubra* across regions relative to the area that is currently climatically suitable. As the underlying idea of consensus models is to incorporate the variation, there cannot be error bars of the variation between single models in the figures.

Bioclimatic models have become one of the most powerful predictive tools for conservation and have been used for a broad range of tasks, including decision making for assisted translocation, design of protected areas, and forecast of climate-change effects and biological invasions (Araújo & Peterson 2012). Because of their ubiquitous use by conservation biologists today and their potential to affect managers, stakeholders, and policy makers (Hannah et al. 2002), it is increasingly important that they generate reliable results. Environmental niche models remain important tools for conservation, despite inherent uncertainty in the spatial projections due to the underlying assumptions shared by all environmental niche models

(Guisan & Thuiller 2005; Sinclair et al. 2010). For example, niche models are based on the assumption that the species is at equilibrium with its environment and therefore that its current distribution reflects the ideal climatic conditions for the species, which can be used to model its potential distribution. Thus, a model of the potential distribution of an invasive species following climate change is based on 2 extrapolations: the first in space (colonization of a different place) and the second in time (following future climate change) (Pearman et al. 2008; Petitpierre et al. 2012). Niche models are also based on the assumption that CS directly translates into a probability of occurrence. Yet, at a local scale it is important

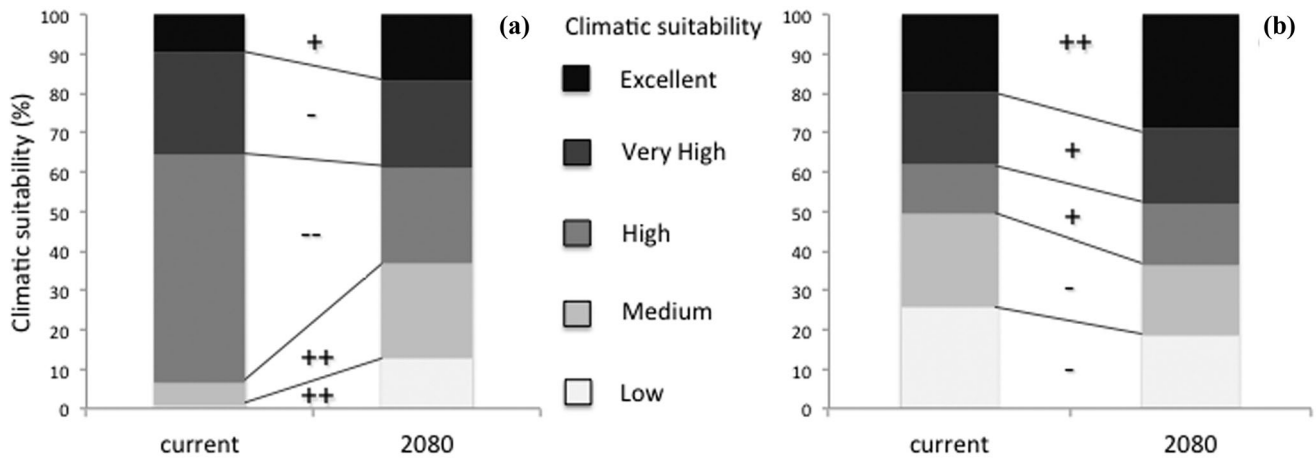


Figure 4. Changes in climate suitability classes (excellent to low as defined in Fig. 1) for (a) *M. destructor* and (b) *M. rubra* following climate change (+ and -, changes of <10%; ++ and --, changes of >10%).

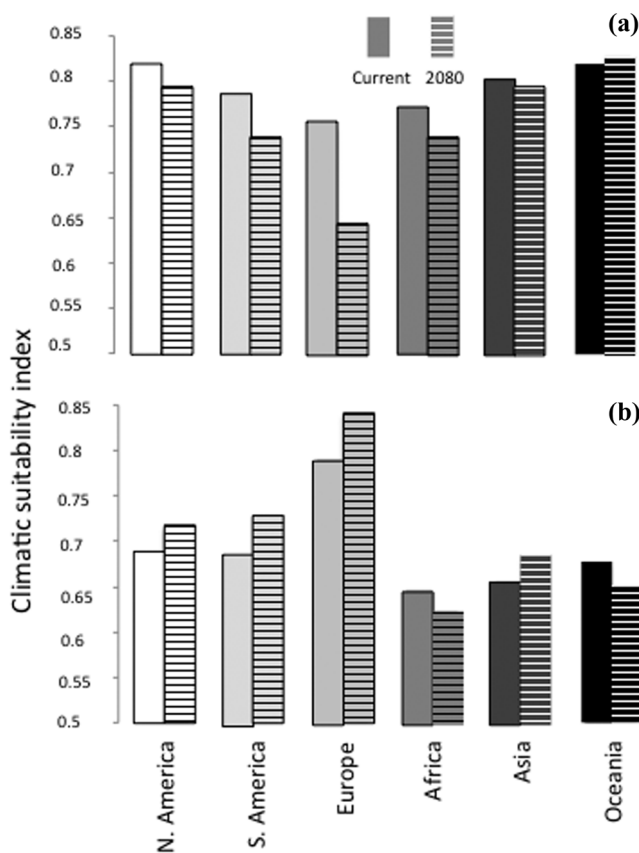


Figure 5. Changes in the climatic suitability index (i.e., quality) in climatically suitable areas across regions following climate change for (a) *M. destructor* and (b) *M. rubra*.

to take into account processes such as the probability of introduction, dispersal mechanisms, species interactions, availability of physical habitat and microclimatic conditions at the site and time of introduction, all of which may contribute to the overall establishment probability

(Sinclair et al. 2010). Nonetheless, bioclimatic models are generally thought to deliver useful approximations (Araújo and Peterson 2012; Warren 2012). Therefore, it is crucial to highlight cases where this approach may lead to an incorrect management decision. Our study provides such an example.

Classically, studies assess the potential distribution of species by quantifying the amount of climatically suitable landmass (e.g., Bakkenes et al. 2002; Thomas et al. 2004; Cheaib et al. 2012), but they generally overlook the level of suitability within these areas. In doing so, the modeler often makes a choice regarding the threshold above which an area is considered suitable (Franklin 2009). There are potentially as many rules for setting thresholds as modeling methods (Nenzén & Araújo 2011), but these rules are usually not based on ecological considerations: the absolute species- and habitat-specific thresholds above which a given species can establish in a climatically suitable area remain generally unknown. Consequently, using one threshold value is often arbitrary and always less informative than using the CS index we introduced here. When forecasts of potential distributions (whether of invasive or protected species) are conducted, it may be crucial to consider that they may not depend only on suitable climatic range but also on the probability of establishment within this range. This is important because a species may fail to establish in a climatically suitable area because it requires not only good but excellent climate conditions to establish in a new ecosystem.

In our case studies, we estimated potential range projections by considering the probability of establishment in addition to a classical binary value of species presence or absence defined by an arbitrary threshold. Although the latter approach predicted no increase of invasion risk for *M. rubra*, the risk of invasion increased for both ant species globally, but for different reasons. For *M. destructor*, a larger suitable climatic range was

predicted, whereas for *M. rubra* the CS of favorable areas was predicted to improve.

The predicted increases of the ant species we studied were unequally distributed among regions. In some regions, invasion risks decreased following climate change, even though it increased globally. Also, increases in their potential distribution were observed at a wide range of latitudes, and these species were not predicted to simply shift to higher latitudes as climate changes, as has been suggested (e.g., Guo et al. 2011). In fact, CS increased in many regions at low latitudes.

Our results support the view that in some cases biological invasions can increase due to climate change (Hellmann et al. 2008; Walther et al. 2009). Beyond the important findings about the 2 major invaders we considered, our results more generally demonstrated the need to use 2 complementary indicators of invasion risk. We recommend assessing the level of CS in addition to the classical (and somewhat arbitrary) binary estimation of climatically suitable areas. This recommendation applies to studies of species under current conditions as well as to projections of suitable conditions in space or in time (e.g., following climate change). The amount of climatically suitable areas decreased for the European fire ant in 4 out of 6 regions, but this was paralleled by a large increase in the level of suitability. Overall, this could result in a net increase in invasion risk globally. This outcome illustrates that it can be crucial to make both quantitative and qualitative assessments to provide a more accurate description of potential species distributions, be they invasive or threatened.

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## Supporting Information

Current distributions of destructor ant and European fire ant (Appendix S1), selected variables and their relative contribution to Maxent (Appendix S2), modeling algorithms (Appendix S3), and a summary of model performances of the 5 modeling methods for the 2 species (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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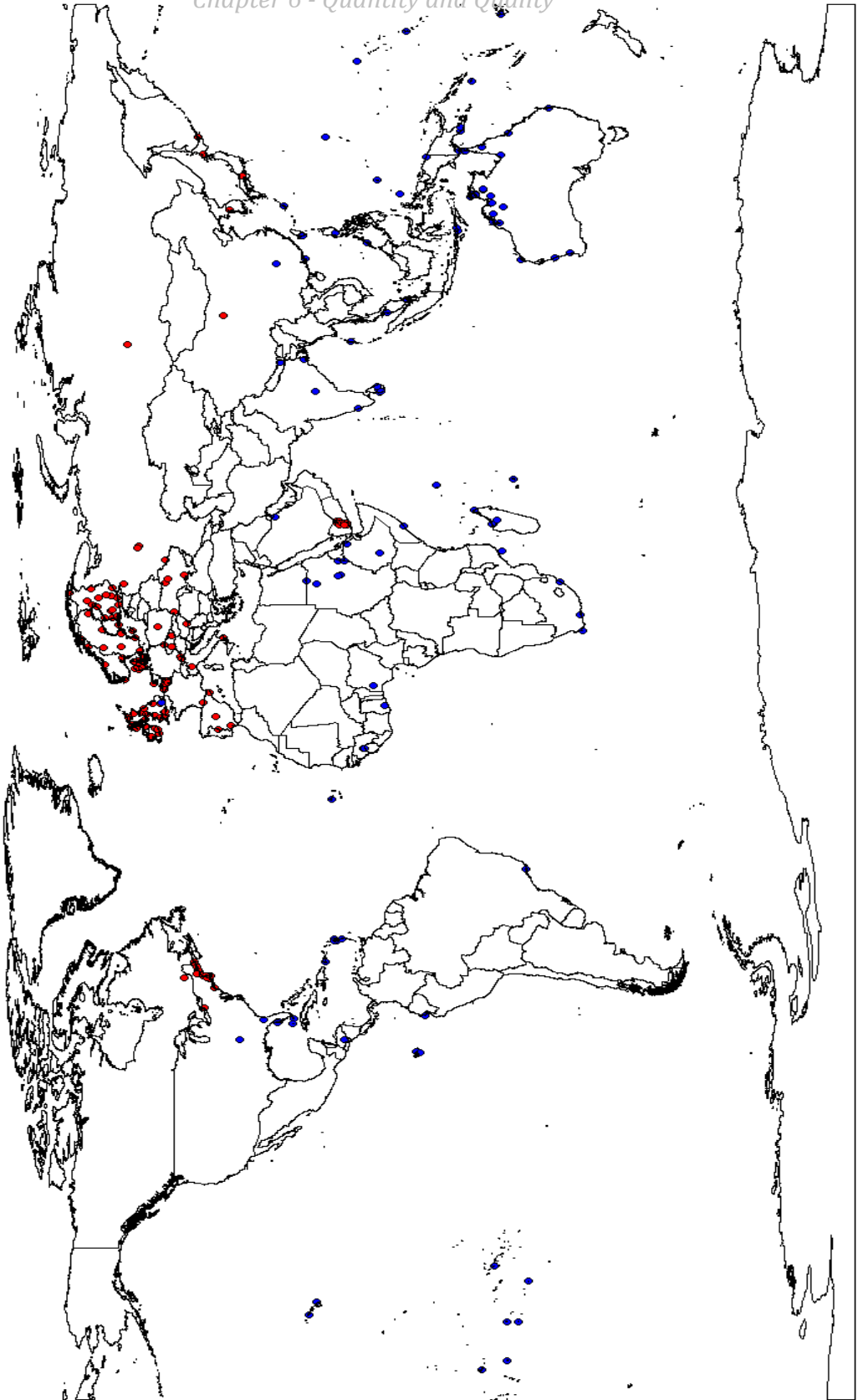


Fig. 1S

Species	Selected Variables	Contribution
<i>M. destructor</i>	Temperature Annual Range	31.7 %
	Min Temperature of Coldest Month	25%
	Mean Diurnal Range (Mean of monthly (max temp - min temp))	13.2%
	Precipitation of Warmest Quarter	7.7%
	Precipitation of Coldest Quarter	4.1%
	Precipitation Seasonality (Coefficient of Variation)	2.3%
<i>M. rubra</i>	Mean Diurnal Range (Mean of monthly (max temp - min temp))	19.7%
	Precipitation of Driest Month	10.9%
	Mean Temperature of Coldest Quarter	9.6%
	Temperature Annual Range	7.1%
	Max Temperature of Warmest Month	4.8%
	Mean Temperature of Wettest Quarter	4.7%

Table S1

Algorithm & Key References	Type of data fitted	Type of outputs/ Functioning	Assumptions	Advantages	Disadvantages	Parameter definitions
1-class Support Vector Machines (SVM-1) Guo et al. 2005 Franklin 2009	Presence	<ul style="list-style-type: none"> <li>Envelope method</li> <li>Hypersphere encloses minimally known presences in the environmental space, analogous to Mahalanobis distance</li> </ul>	Species niche concept as a portion of environmental hyperspace	<ul style="list-style-type: none"> <li>Particularly effective for presence only data</li> <li>Robust with few occurrence points</li> <li>Can fit complex shapes</li> <li>Less sensitive to outliers than other envelope methods such as BIOCLIM or HABITAT</li> </ul>	<ul style="list-style-type: none"> <li>Tend to predict a much larger area than other kinds of models (but this can be an advantage when minimizing omission error is important)</li> <li>Impossible to visualize classification rules and verify ecological meaning of the output</li> </ul>	<p><b>Kernel</b> = The function that allows to fit hyperplanes in high-dimensional feature space, which can be non-linear in the original input space.</p> <p>The implemented Kernel function is the most commonly used Gaussian <b>Radial Base Function</b> because of their localized responses</p> <p><b>Y</b> = a coefficient of the kernel function. Set to be 1/k where k is the number of involved factors</p> <p><b>Nu</b> = Indicates a lower bound of the fraction of Support Vectors and is set to be the default option 1.</p>
2-class Support Vector Machines (SVM-2) Guo et al. 2005 Drake et al. 2006 Scholkopf et al. 1999 Cristianini N, Scholkopf B 2002	Presence-absence	<ul style="list-style-type: none"> <li>Probability density function</li> <li>Envelope</li> <li>Fit hyperplanes separating presence/absence classes</li> </ul>		<ul style="list-style-type: none"> <li>Lowest omission error compared with other models (Drake et al. 2006)</li> <li>Can fit complex shapes</li> </ul>	<ul style="list-style-type: none"> <li>Impossible to visualize classification rules and verify ecological meaning of the output</li> </ul>	<p>A <b>cost</b> parameter C controls the trade-off between allowing some misclassifications and forcing rigid margins. To avoid over-fitting, C is set so that the model fits maximally the data, without degrading the cross-validated AUC values.</p>

Table S2

## Table References

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Ant species	Modelling technique	AUC
<i>M. destructor</i>	1 class SVM	<b>0,793</b>
	2 class SVM	<b>0,886</b>
	ANN	<b>0,906</b>
	Maxent	<b>0,875</b>
	CT	<b>0,968</b>
<i>M. rubra</i>	1 class SVM	<b>0,879</b>
	2 class SVM	<b>0,922</b>
	ANN	<b>0,933</b>
	Maxent	<b>0,977</b>
	CT	<b>0,951</b>

Table S3



# Global warming may freeze the invasion of big-headed ants

Cleo Bertelsmeier, Gloria M. Luque and Franck Courchamp





# Global warming may freeze the invasion of big-headed ants

Cleo Bertelsmeier · Gloria M. Luque ·  
Franck Courchamp

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**Abstract** Climate change and invasive species are two of the most serious threats of biodiversity. A general concern is that these threats interact, and that a globally warming climate could favour invasive species. In this study we investigate the invasive potential of one of the “100 of the world’s worst invasive species”, the big-headed ant *Pheidole megacephala*. Using ecological niche models, we estimated the species’ potential suitable habitat in 2020, 2050 and 2080. With an ensemble forecast obtained from five different modelling techniques, 3 Global Circulation Models and 2 CO<sub>2</sub> emission scenarios, we generated world maps with suitable climatic conditions and assessed changes, both qualitatively and quantitatively. Almost one-fifth (18.5 %) of the land-mass currently presents suitable climatic conditions for *P. megacephala*. Surprisingly, our results also indicate that the invasion of big-headed ants is not only unlikely to benefit from climate change, but may even suffer from it. Our projections show a global decrease in the invasive potential of big-headed ants as early as 2020 and becoming even stronger by 2080 reaching a global loss of 19.4 % of area with favourable climate.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10530-012-0390-y) contains supplementary material, which is available to authorized users.

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The decrease is observable in all 6 broad regions, being greatest in the Oceania and lowest in Europe.

**Keywords** Biological invasions · Climate change · *Pheidole megacephala* · Niche modelling · Ensemble forecast · Big-headed ant

## Introduction

Invasive species are generally considered the second most serious threat to global biodiversity and rates of exotic species introductions are ever increasing with human trade and tourism (Vitousek et al. 1997). As a consequence, many native species are displaced, leading to local extinctions of fauna and flora. This ultimately affects community structures and can severely impair ecosystem functioning. Ants are among the worst invasive species (Rabitsch 2011; Holway et al. 2002; Lach and Hooper-Bui 2010). Because they are small, numerous and colonial, they can rapidly colonize a new habitat. One of the most important factors limiting their distribution is climate (Roura-Pascual et al. 2011; Dunn et al. 2009; Sanders et al. 2007; Jenkins et al. 2011) because many features of their biology are temperature or humidity dependent, such as foraging (Brightwell et al. 2010), oviposition rates (Abril et al. 2008), survival (Walters and Mackay 2004), colony dynamics, the structure of foraging networks (Heller and Gordon 2006) and

dominance over other species (Suwabe et al. 2009). It is therefore crucial to assess their invasive potential under climate change.

Several studies suggest that climate change could exacerbate the threat posed by invasive species, especially poikilotherms, by removing thermal barrier and allowing them to establish at higher latitudes (Brook et al. 2008; Dukes and Mooney 1999; Sala et al. 2000; Walther et al. 2009; Hellmann et al. 2008). Here, we assess the impact of climate change on the potential distribution of the big-headed ant, *Pheidole megacephala*, which is listed among the “100 of the worst invasive species” by the IUCN (Lowe et al. 2000). The species is believed to be native to southern Africa and has already invaded various types of habitats worldwide, such as agricultural areas (Wetterer 2007; IUCN SSC Invasive Specialist Group 2012), coastland (Fisher 2012), forests (Fisher 2012; Hoffmann et al. 1999), riparian zones (IUCN SSC Invasive Specialist Group 2012), shrub lands (Wetterer 2007; IUCN SSC Invasive Specialist Group 2012), wetlands (IUCN SSC Invasive Specialist Group 2012; Fisher 2012) and urban areas (Wetterer 2007; IUCN SSC Invasive Specialist Group 2012; Fisher 2012). Although the species is frequently associated with disturbed habitats, it has also been found to invade undisturbed open forests, displacing dominant ant species (Holway et al. 2002) and causing the local loss of several functional groups of ants (Vanderwoude et al. 2000). *Pheidole megacephala* is very aggressive towards other ant species and has a heightened ability to recruit efficiently many workers and to raid nests of competing ant species (Holway et al. 2002; Dejean et al. 2008). Moreover, it is a highly efficient predator that can capture a wide range of prey, including large invertebrates (Dejean et al. 2007a, b). Where it occurs at high densities, few native invertebrates persist (Wetterer 2007). In a tropical rainforest in Australia *P. megacephala* abundance was 37–110 times greater than of all the native ants in uninfested sites (Hoffmann et al. 1999). Its negative ecological impact is likely to be greater than that of any other invasive ant species (Wetterer 2007) and only very few successful eradications have been achieved (Hoffmann 2010). As management of invasive ants is notoriously difficult, it is better to take preventive actions and carry out invasion risk assessments in advance, which should include an evaluation of climatic suitability (Hoffmann and Parr 2008).

However, despite its huge consequences for invaded ecosystems, no study so far has assessed the species’ current invasive potential area and its trend in the future following climate change.

In this study, our aims are

1. To make global predictions of landmass presenting a currently favourable climate for *P. megacephala*.
2. To estimate the amount of global favourable area under 2 different scenarios of climate change (A2a and B2a) for three points in the future (2020, 2050, 2080) and to quantify the change in the amount of suitable habitat compared to today.
3. To quantify the regional impact of climate change on the potential habitat—taking 6 broad geographic regions as a proxy (N. America, S. America, Europe, Africa, Asia, Oceania).

In order to model the species’ potential habitat, we use ecological niche models, which explain the species’ distribution with a set of climatic predictor variables. In recent years, an increasing number of modelling techniques have become available and it has been shown that spatial predictions are sensitive to the choice of modelling algorithms. Furthermore, predictions for future climatic conditions are sensitive to the choice of the Global Circulation Model (GCM) used. To deal with this variability and in order to separate the “signal” from the “noise”, one can develop “ensemble forecasts” that define areas of consensual prediction (Araújo and New 2007; Roura-Pascual et al. 2009). We combined models using five different modelling techniques and three GCMs for two Special Report on CO<sub>2</sub> Emission Scenarios (SRES) and for four points in time (current, 2020, 2050, 2080). We then compare quantitatively the change in time of suitable areas, both globally and regionally.

## Materials and methods

### Species distribution data

Ecological niche models search for a non-random association between environmental predictors and species occurrence data to make spatial predictions of the species’ potential habitat. Because the models should include the full set of climatic conditions under which the species can thrive, we decided to include

occurrence points from both its invaded and native range (following (Liu et al. 2011; Rödder and Lötters 2009; Beaumont et al. 2009; Broennimann et al. 2007)). It has been shown that models calibrated based on only native range data often misrepresent the potential invasive distribution and that these errors propagate when estimating climate change impacts (Beaumont et al. 2009; Broennimann et al. 2007).

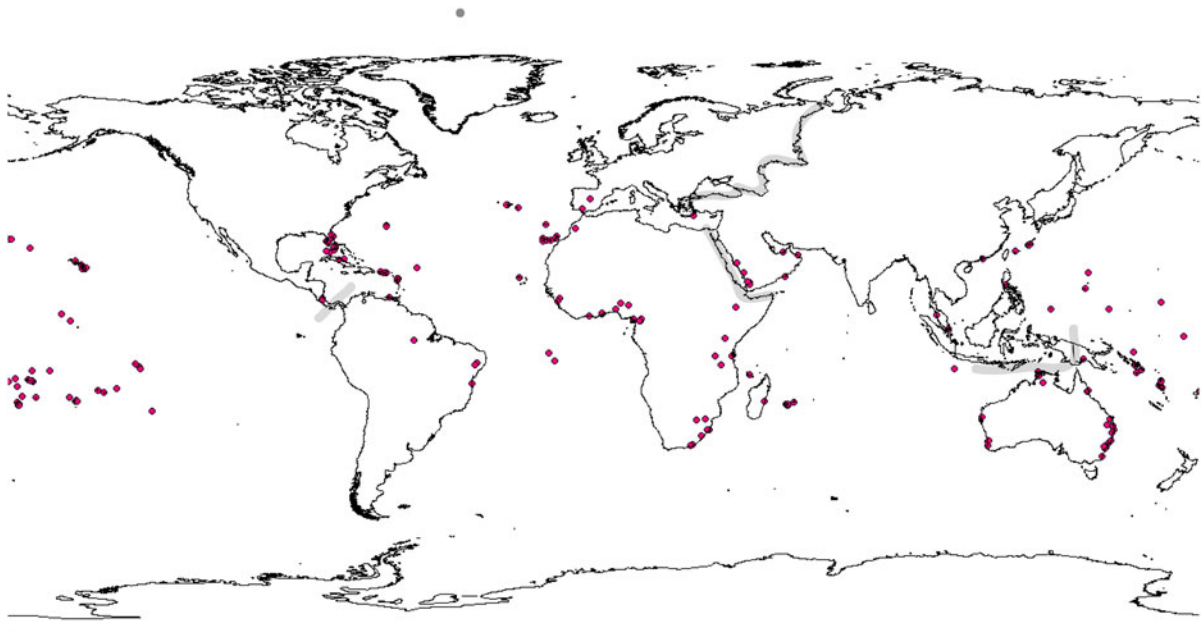
In total, 208 occurrence records (Fig. 1) were used from the literature, researchers, government agencies, student projects and private collectors, compiled by a public database for ant distributions (Harris and Rees 2004). The species has achieved a pantropical distribution and is known to thrive in tropical and subtropical, warm-temperate and Mediterranean regions (Hoffmann et al. 1999). Therefore, we have removed points, which are clearly outside these climatic conditions and are very likely to be either spurious records or based on indoor locations.

In order to make robust range projections of a species' niche, it is not necessary to include every single location where the species is present but one should aim for a representative cover of all climatic conditions under which the species is known to exist. Our occurrence records come from all continents (except Antarctica, where the species does not occur) and include tropical

and temperate locations, over a wide range of latitudes. For models requiring absence data, 10,000 randomly chosen pseudo-absence points were generated from all around the world to provide background data.

#### Climatic predictors

We modelled the species' niche based on the 19 bioclimatic variables provided by the Worldclim database (Hijmans et al. 2005). These are frequently used in studies on climatic niches of species and impacts of climate change on species distributions because they have been constructed to have a biological meaning (Wolmarans et al. 2010). The full set of bioclimatic variables was used as model input because the machine learning methods used for niche modelling implicitly deal with variable selection and are unlikely to be improved—and may even be degraded by external modelling methods to pre-select variables (Elith et al. 2011, Guyon and Elisseeff 2003). Machine learning methods are a set of algorithms that learn the mapping function or classification rule inductively from the input data. They use cross-validation to test model performance on held-out data within the modelling process (Elith et al. 2006). The bioclimatic variables (full list in the Electronic Supplementary



**Fig. 1** Documented occurrences of *P. megacephala* in its native and invaded range (red dots). The grey lines indicate the boundaries between the geographic regions that we used for the analysis of favourable habitat. (Color figure online)

Material, fig. S1) are derived from monthly temperature and rainfall values from 1960 to 1990 (Hijmans et al. 2005). They represent annual trends (e.g. mean annual temperature, annual precipitation), seasonality (e.g. annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g. temperature of the coldest and warmest month, and precipitation of the wet and dry quarters) (Hijmans et al. 2005). We used a spatial resolution of 10 arcmin (approx.  $18.5 \times 18.5$  km pixel).

Future climatic data was provided by the 4th IPCC assessment report (GIEC 2007). The projections are calibrated and statistically downscaled using the WorldClim data for ‘current’ conditions and therefore the projections can be compared. In order to consider a range of possible future climates, we modelled the species’ potential future distribution based on down-scaled climate data from three different GCMs provided by different climate modelling centres: The CCCMA-GCM2 model, the CSIRO-MK2 model and the HCCPR-HADCM3 model (GIEC 2007). In addition, projections for two different SRES CO<sub>2</sub> emission scenarios were included in our models: the optimistic B2a scenario (CO<sub>2</sub> concentration 800 ppm, 1.4–3.8 °C temperature increase) and the pessimistic A2a scenario (CO<sub>2</sub> concentration 1,250 ppm, 2–5.4 °C temperature increase) (GIEC 2007).

### Ecological Niche Modelling

Five different machine learning modelling techniques were used to generate the ensemble forecasts. Machine learning methods are among the recently developed tools especially designed for prediction (Lorena et al. 2011) and it has been claimed that their predictive performance exceeds that of more conventional techniques (Elith and Leathwick 2009).

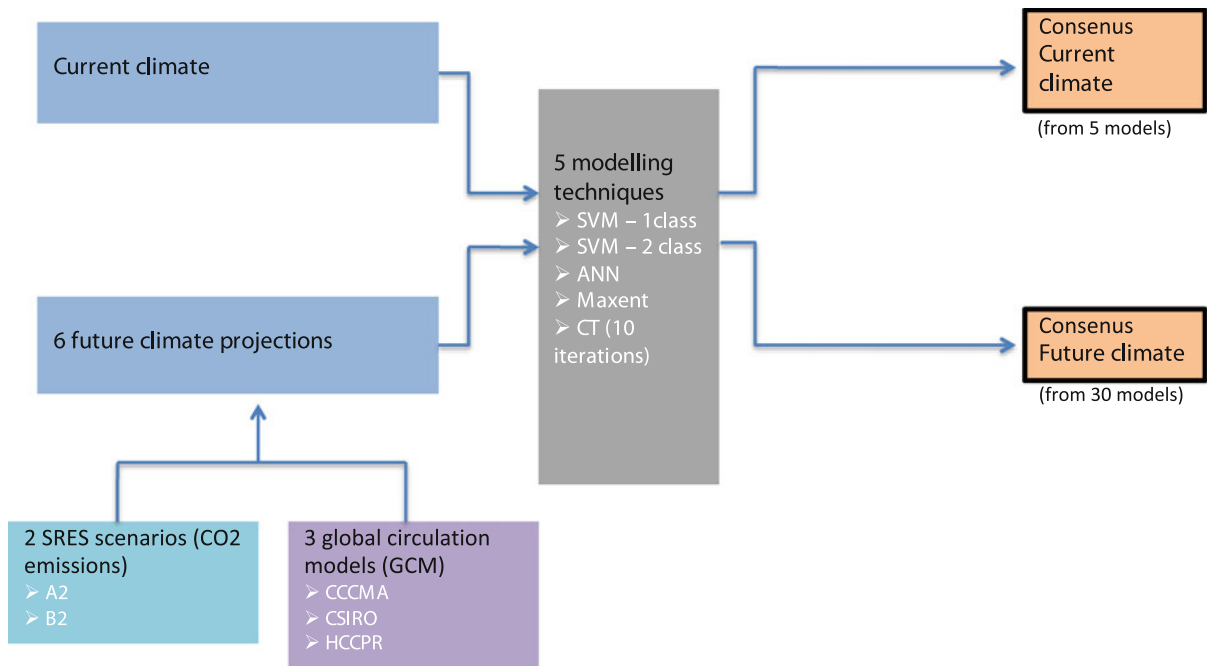
All models were run using the ModEco Platform with default parameters (Guo and Liu 2010). The first two models are using a new generation of learning algorithms: Support Vector Machines (SVMs) (Cristianini and Schölkopf 2002; Guo et al. 2005), 1-class-SVMs (parameters: kernel = Radial Base function,  $\gamma = 1$ ,  $\nu = 0.05$ ) and 2-class-SVMs (parameters: type = C\_SVC, kernel = Radial Base function,  $\gamma = 3$ , Cost = 1). In addition, we used Artificial Neural Networks (ANN) (parameters: type = Back-propagation ANN, Momentum = 0.3, Learning rate = 0.1) (Manel et al. 1999; Franklin 2009;

Maravelias et al. 2003) and Classification Trees (CT) (parameters: type = iterative, Number of trials = 5, Window size = 10, Pruning level = 0.25) (De’ath and Fabricius 2000). The result was an average across 10 Classification Trees iterations of the model algorithm. Finally, we used the Maximum Entropy method (Maxent), a common model algorithm for niche modelling (Stiels et al. 2011; Jimenez-Valverde et al. 2011; Murray et al. 2011; Jarnevich and Reynolds 2011; Bradley et al. 2010; Ficetola et al. 2010; Ward 2007; Roura-Pascual et al. 2009, Phillips et al. 2006).

Although these machine-learning methods are known for their high predictive power, there are comparatively few tools available for visualizing and analysing the contribution of different variables. This is partly because techniques such as ANN’s create synthetic variables from the original set, leading to a complex and “black box” nature of the model (Elith and Leathwick 2009). Maxent is one of the few machine-learning models to possess techniques for ecological insight. Therefore, we present jackknife tests of variable contribution in Maxent, to indicate which factors are most important in determining the current distribution of the species (Phillips et al. 2006).

The different modelling techniques, SRES scenarios and GCMs are used in different combinations in order to obtain a range of possible future habitat maps (Fig. 2). In a second step, the individual models were combined into consensus models reducing uncertainties of each of the models. The idea of consensual forecasts is to separate the signal from the “noise” associated with the errors and uncertainties of individual models, by superposing the maps based on individual model outputs. Areas where these individual maps overlap, are defined as areas of “consensual prediction” (Araújo and New 2007). This is different from averaging the individual projections, as the area predicted by the consensual forecast can be smaller than any individual forecast if there is little spatial agreement (i.e. overlap) between individual forecasts. Simple averaging across individual forecasts is considered unlikely to match the reality and therefore ensemble averages or confidence limits for the consensual prediction are classically not calculated (Araújo and New 2007).

The individual model outputs (i.e. the probability of presence in each pixel) were weighted according to their AUC in order to enhance the contribution of models with higher model performance values (see



**Fig. 2** Model design to obtain estimates of areas of suitable habitat for *Pheidole megacephala* in the present and in the future. The species' potential future distribution is modelled using 2 CO<sub>2</sub> emission scenarios, 3 climate models (GCM) and

five modelling methods, yielding a total of 30 individual models that were combined in the total consensus model. This process was repeated three times, in order to get projections for 2020, 2050 and 2080

(Roura-Pascual et al. 2009)). We obtained a continuous projection of the consensus model with a probability of the species being present assigned to each pixel.

Ensemble models were generated for current climate (consensus across models using the five modelling techniques), for the A2 scenario (consensus including 15 individual projections in total with climate data from 3 GCMs and 5 modelling techniques) and for the B2 scenario (again 3 × 5 projections). A total climate change forecast model was also generated, including all 30 individual projections—each based on a different combination of CO<sub>2</sub> scenario × GCM × modelling technique. This yields a consensus projection for one particular point in time (see Fig. 2). Consequently we obtained a single value per consensus model, which we decided to illustrate later in the form of histograms. But as the underlying idea of consensus models is to incorporate the variation, there cannot be error bars of the variation between single models in the figures. The modelling process was repeated to generate consensus predictions for 2020, 2050 and 2080).

#### Assessing favourable habitat

Potential habitat suitability was assessed in two ways. First, a classical threshold rule was applied, whereby all pixels in which the probability of presence exceeded 0.5 were classified as “favourable” habitat (Franklin 2009). This is frequently used for binary classification in the context of species distribution modelling (Franklin 2009; Klamt et al. 2011). For specific uses of our models, it might be interesting to minimize the chance of either over- or under-prediction of potential habitat (omission or commission errors) and to apply a different threshold. For example, for management decisions it could be better to apply a more “prudent” (lower) threshold that lowers the probability of omission errors. To allow these user-specific applications of our models, we also provide maps with a continuous output with a probability of presence between 0 and 1 (with 0.1 intervals), although we consider only habitat as favourable above a probability of presence of 0.5. Spatial analyses were carried out using DIVA-GIS program, developed by Hijmans et al. (2001).

Second, in order to evaluate whether the “quality” of the available habitat has changed, we divided the “favourable” habitat into five classes, ranging from “low” ( $0.5 < p < 0.6$ ) to “excellent” suitability ( $0.9 < p < 1$ ) and compared change of classes over time.

### Model validation

Model robustness has been evaluated with the AUC of the ROC curve, which is a nonparametric threshold-independent measure of accuracy that is commonly used to evaluate species distribution models (Ward 2007; Roura-Pascual et al. 2009; Manel et al. 1999; Pearce and Ferrier 2000). We used the AUC because it is not a measure of model performance that depends on the classification threshold, which has been selected, and is easily interpretable as the probability that a model discriminates correctly between presence and absence points (Pearce and Ferrier 2000; Roura-Pascual et al. 2009). AUC values can range from 0 to 1, where a value of 0.5 can be interpreted as a random prediction. AUC between 0.5 and 0.7 are considered low (poor model performance), 0.7–0.9 moderate and  $>0.9$  high (Franklin 2009 and references therein). In addition, several threshold-dependent measures were used to summarize model performance, including sensitivity (proportion of correctly classified presences), specificity (proportion of correctly classified absences), overall accuracy (proportion correctly classified presences and absences) and Cohen’s Kappa (Fielding and Bell 1997). Kappa ranges from  $-1$  to  $1$  and values of  $0$  are no better than produced by chance. In general, models with a Kappa  $> 0.4$  are considered to be good (Fielding and Bell 1997).

In addition, a one-way ANOVA was conducted using R software version 2.12.2 to compare differences in individual model forecasts due to differences in CO<sub>2</sub> emission scenarios, GCMs and modelling methods.

## Results

Models achieved good to excellent performance with AUC ranging from 0.865 to 0.981 and Kappa ranging from 0.534 to 0.793. That indicates overall a good to very good ability to predict the species presence (Table 1). There was no significant difference between projections under different CO<sub>2</sub> emission

scenarios [ $F_{(1,28)} = 0.01$ ,  $p = 0.945$ ). The difference between projections based on different GCMs [ $F_{(2,27)} = 3.87$ ,  $p = 0.033$ ] and different modelling methods [ $F_{(4,25)} = 12$ ,  $p < 0.001$ ] were significant, but all individual models were showing the same trend (Fig. S2, Electronic Supplementary Material). The jackknife test of variable importance carried out with Maxent shows that the climatic variable with the best predictive power when used in isolation is “temperature annual range” (max temperature of the warmest month minus min temperature of the coldest month). Its percentage contribution to the final Maxent model is 24.7 %. The variable that decreases the gain most when omitted is “temperature seasonality” (for variable description see (Hijmans et al. 2005)), with a permutation importance of 25.8 %. Both, “temperature annual range” and “temperature seasonality” are negatively related to occurrence of the species, i.e. *P. megacephala* is more likely to occur in places with relatively low temperature range and variability. Further, the third and fourth most important variables were “diurnal range” and “precipitation of the coldest quarter”, which have a percentage contribution to the final Maxent model of 14.5 % and 9.1 % respectively.

### Current potential habitat worldwide

Under the current climate, the ensemble forecast model predicts that 18.5 % of global landmass presents favourable climatic conditions potentially allowing the species to establish, with 4.9 % of total landmass presenting low suitability, 4.8 % medium, 2.4 % high, 3.5 % very high and 2.8 % excellent suitability.

The greatest proportion of favourable area is found in South America, Africa, Oceania and Asia (in that order of importance), whereas relatively little suitable habitat is found in Europe and North America (4.1 % and 4.5 % of the total suitable area, respectively, Fig. 3a). Currently the species is already a global invader and established on all continents. However, this shows that it could expand much further, especially in the regions that present a high percentage of climatically favourable landmass. The total favourable landmass is unequally distributed among the continents (Fig. 3b), only 1 % of the total favourable landmass for the species is found in Europe, 5 % in North America, 13 % in Asia, 17 % in Oceania, 30 % in South America and 34 % in Africa.

**Table 1** Summary of model performances of the five machine learning algorithms

Modelling technique	AUC	Sensitivity	Specificity	Kappa	Overall accuracy
1 Class SVM	0.872	0.784	0.75	0.534	0.767
2 Class SVM	0.865	0.793	0.808	0.601	0.8
ANN	0.955	0.649	0.923	0.572	0.897
Maxent	0.921	0.736	0.86	0.596	0.798
CT	0.981	0.832	0.962	0.793	0.897

### Favourable habitat following climate change

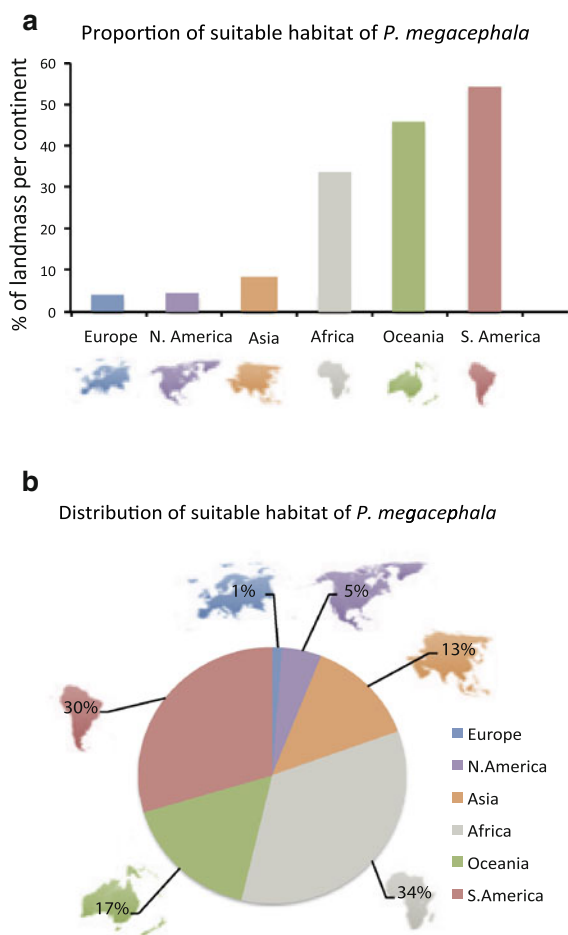
The amount of potential habitat is clearly decreasing by 2080 under either CO<sub>2</sub> emission scenarios, A2 and B2 (Fig. 4a, b). The overall decrease of potential habitat relative to the current potential habitat is  $-21\%$  under the A2 scenario,  $-17\%$  under B2 scenario and  $-19.4\%$  in the overall consensus model that combines forecasts under both scenarios. Moreover, among areas that still present a suitable climate, one can also observe a clear change in the “quality” of the habitat, with “excellent” and “very high suitability” areas both decreasing (Fig. 5a).

Overall, the potential habitat is predicted to decrease in all of the 6 broad geographic regions, but the magnitude of this decrease varies. The loss of potential habitat is highest in the Oceania region ( $-28\%$ ), followed by North America ( $-27\%$ ), South America ( $-18.8\%$ ), Africa ( $-18.8\%$ ), Europe ( $-13.7\%$ ) and Asia ( $-9.2\%$ ) (Fig. 5b).

Suitable climatic conditions are steadily decreasing over time for *P. megacephala*. Compared to current suitable area, its potential habitat will decrease globally by  $11.1\%$  in 2020, by  $15.5\%$  in 2050 and by  $19.4\%$  in 2080 (Fig. 5c).

### Discussion

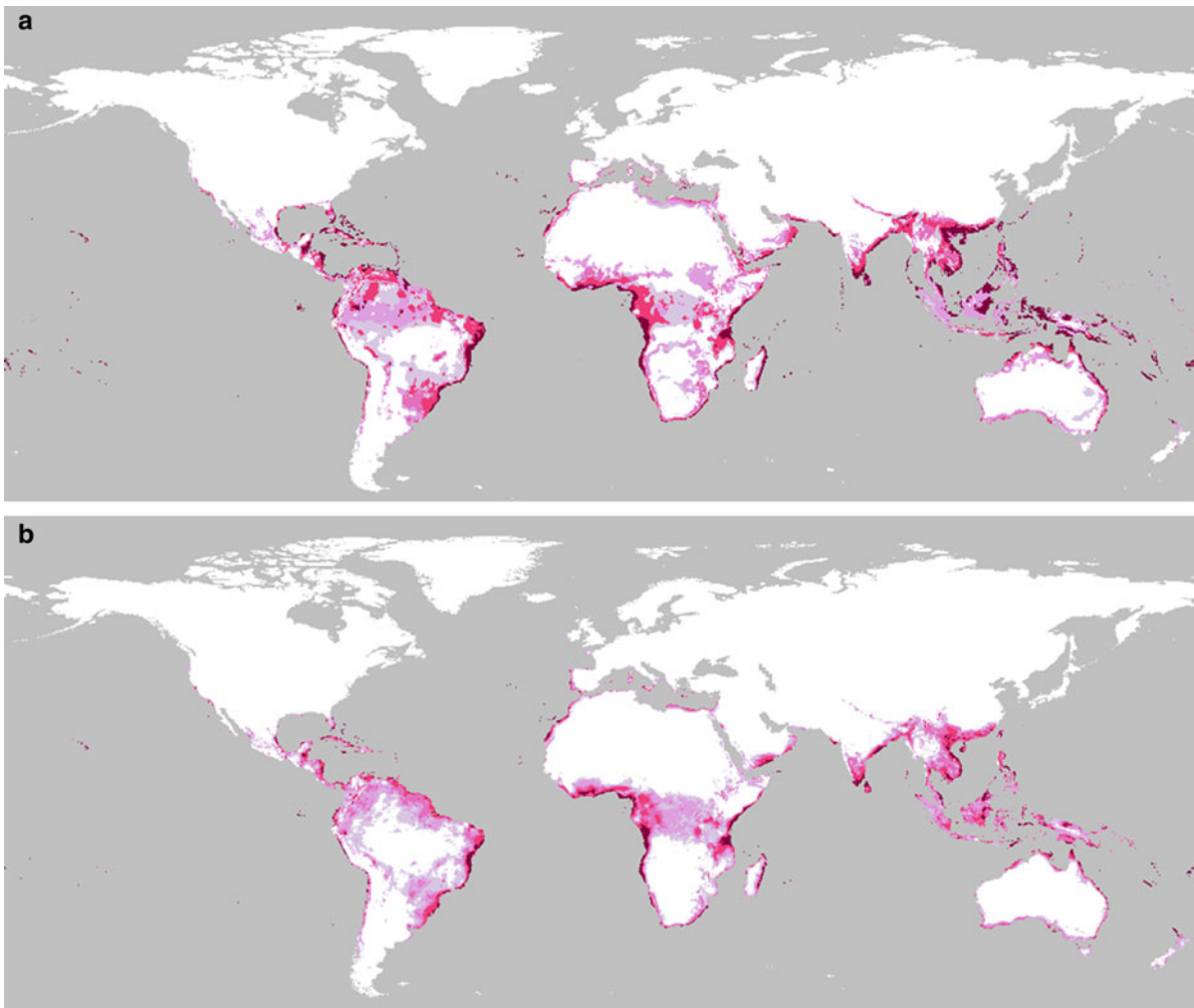
The ensemble forecasts predict that nearly a fifth of global landmass ( $18.5\%$ ) is currently climatically suitable for *P. megacephala*, which is worrying given the dramatic impact this invader is known to cause (e.g. Wetterer 2007; Vanderwoude et al. 2000; Hoffmann and Parr 2008). South America is the continental region with the currently largest proportion of suitable habitat ( $54\%$  South American landmass is favourable) and Europe is the lowest ( $4.1\%$ ). However, the projections following climate change show very



**Fig. 3** Regional distribution of suitable areas of *P. megacephala*: **a** proportion of each region that is suitable, **b** distribution of suitable areas per region

surprising results. Contrary to what is generally believed, our results suggest that climate change will not increase invasion risks of *P. megacephala*. On the contrary, the potential habitat will decrease, leading to a substantial loss of global suitable habitat, varying



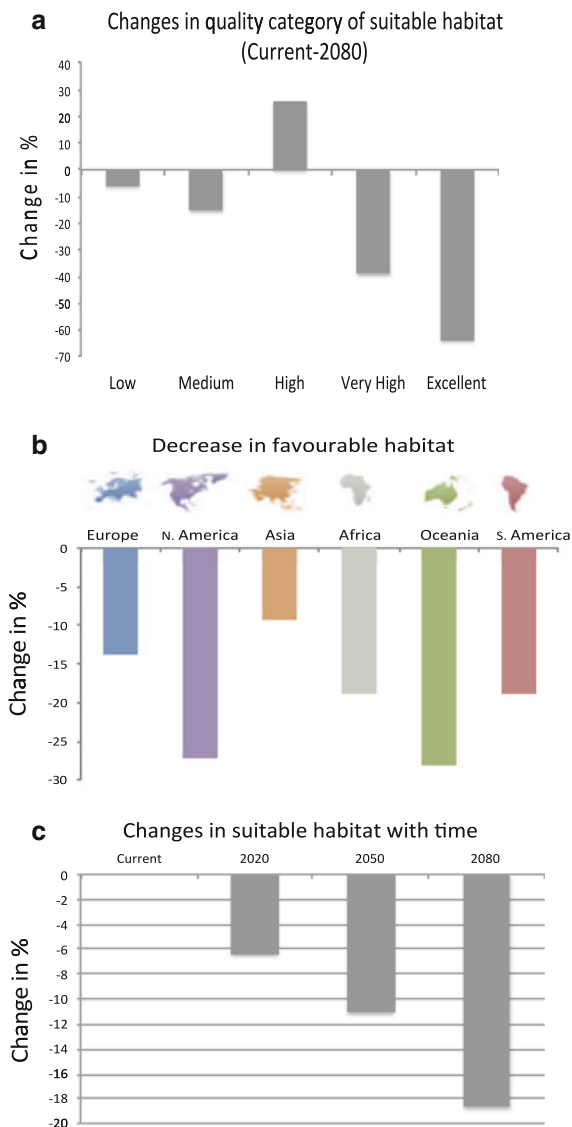


**Fig. 4** Maps of potential habitat. Climatic suitability ranges from “low” (*light red*) to “excellent” (*dark red*). **a** Current climatic conditions. **b** Consensus model of A2 + B2 scenario. (Color figure online)

between 17 and 21 % (depending on the scenarios of climate change considered, A2 or B2). In addition, the decrease in potential habitat can be seen all over the world, although it is heterogeneous across the 6 continental regions considered. It is highest in the Oceania region (−28 %) and lowest in Asia (−9.2 %). Loss of potential habitat can be seen as early as 2020 but will be accentuated by 2050 and even more so by 2080.

These results might help focus management and conservation efforts, in particular by providing regional information on the relative risk of invasion of this species. Overall, the decrease in global favourable landmass of one of the worst invasive

species (Lowe et al. 2000) is encouraging for conservation. However, it should be kept in mind that the metric used here is potential (current and future) habitat of suitable climatic conditions, and not actual invaded areas, neither current nor future. That means that the potential habitat of the species is greater than its actual distribution. Consequently, even though it will decrease, it is possible that the future potential habitat will still be greater than the current distribution of the species. Overall, one might therefore observe a range increase of the species by 2080 compared to the current distribution. However, this increase could have been much greater if climate change had not reduced the potentially favourable landmass.



**Fig. 5** **a** Changes in the future potential habitat relative to current potential habitat (in %). The different categories reflect the «quality» of the potential habitat under the consensus climate change model. There are no *error bars* because a consensus model has been used. **b** Change (in %) of favourable habitat in the six geographic regions. **c** Change of potential habitat over time

In addition, interpretation of these results should be made in awareness of the set of strong assumptions classically made by using niche models (Guisan and Thuiller 2005; Austin 2007). For example, all niche models assume niche conservation, which implies that the species is at equilibrium with its environment and will not change its requirements in space (new

potential habitat) or time (future climate scenarios). However, invasive species may have non-equilibrium distributions (Sutherst and Bourne 2009) and expand into these non-analogue climates, which can be accompanied by a niche shift or filling of a pre-adapted niche (Petitpierre et al. 2012; Webber et al. 2012). There are documented cases of niche shifts in invasive species following genetic bottlenecks or rapid evolution in the new habitat leading to an invasive niche that differs from the native niche (Gallagher et al. 2010; Broennimann et al. 2007; Pearman et al. 2008) (but see (Fitzpatrick et al. 2007)).

Moreover, it is possible that the current distribution of the species is not limited only by climatic factors. A general weakness of niche modelling is that biotic interactions are not taken into account. However, a global analysis of the relative role of different determinants of invasion success of the Argentine ant has shown that biotic resistance had a very weak influence in regions with high climatic suitability. Biotic interactions became important in determining invasion success only in less climatically favourable regions (Roura-Pascual et al. 2011). It can be argued that in the case of many invasive species, and in particular *P. megacephala*, native fauna has been shown not to resist much and therefore the distribution of the species is probably not much limited by natural enemies, including competitors (Roura-Pascual et al. 2011; Dejean et al. 2007b, 2008; Hoffmann and Parr 2008).

Our aim here was to produce forecasts at a global scale, at which climate is the most important factor determining the distribution of invasive ants (e.g. Roura-Pascual et al. 2011; Dunn et al. 2009; Sanders et al. 2007; Jenkins et al. 2011). However, if one aims to produce more models at a very fine scale, it will enhance model precision to include additional variables—especially human modification of habitats (Roura-Pascual et al. 2011). Microclimate may also be an important factor to consider at a smaller scale. For example, it has been shown that the abundance of invasive Argentine ants increased in plots with increased moisture levels due localized watering of plants (Menke and Holway 2006). Furthermore, the nest of the ant colony can play an important role in providing a thermal refuge, as the temperature experienced by the colony at the micro-habitat scale can be different from the air temperature recorded by climate stations (Ward 2007).

Many uncertainties are associated with the models of future climatic conditions under different scenarios

of global climate change and different CO<sub>2</sub> emission scenarios. Different assumptions in atmospheric physics can lead to substantially different GCMs. These divergences are classically considered as “noise” and consensus models are used to get a picture of the general tendency (Araújo and New 2007). We took into account a wide range of possible future climatic conditions by choosing three of the most widely used GCMs and two CO<sub>2</sub> emission scenarios. Similarly, to account for variability in the projections due to different modelling algorithms, we included five different modelling techniques that have all been applied to ecological modelling. Our results show that these models achieved good to excellent performance in their ability to predict the species presence.

The “signal” from the consensus models is that an enormous area, which represents approximately 1/5 of global landmass, currently has favourable climatic conditions for *P. megacephala*, which may allow the species to extend its invasive range further than it already has. Even though this global invader is present on all continents, it is likely that it will spread further, with devastating impacts on local biodiversity. However, climate change will not exacerbate this. On the contrary, *P. megacephala* will suffer a substantial loss of potential habitat in all regions and over all time steps considered following climate change. This is opposite to classical views of global climate change exacerbating the effects and increasing the ranges of many invaders, especially those currently limited by climate. The general consensus has been that invasive species will follow a path opposite to the rest of the biodiversity in the future, thereby interacting synergistically with climate change to increase the overall threat on biodiversity (Brook et al. 2008; Dukes and Mooney 1999; Sala et al. 2000; Walther et al. 2009; Hellmann et al. 2008). Our results show this is not necessarily the case. In fact, it may well be that many invasive species will follow the global trend of biodiversity in general, which is predicted to decrease substantially (Bellard et al. 2012). In this regard, only very few studies so far have suggested that some invasive species could also decrease following climate change (Walther et al. 2009). However, one other invasive ant known for its devastating impacts, the Argentine ant (*Linepithema humile*) might similarly show a moderate decline by 2050 (Roura-Pascual et al. 2004; Cooling et al. 2011). But the Argentine ant may lose habitat due to “geometric” reasons because its climatic envelope

will shift to higher latitudes, expanding towards the poles and shrinking at tropical latitudes. *Pheidole megacephala*, on the other hand, will experience very little shifts in potential habitat. The envelope presenting favourable climatic conditions will mostly shrink.

Therefore, it is possible that the worst invasive species of today may not be the worst invasive species of tomorrow. Given this unexpected result, it would be interesting to carry out more studies on invasive species to assess potential trends of invasive species following global change.

An important conclusion from this study is that devastating invasive species like *P. megacephala* may fail to invade some areas where the habitat is currently suitable. Therefore, despite clear, negative impacts on biodiversity globally (Bellard et al. 2012), climate change could also have an indirect positive effect on some aspects, for example by reducing the potential range of problematic species that are the cause of numerous local species extinctions. Management efforts to control *P. megacephala* should continue, as a very large proportion of the Earth’ landmass is currently favourable. Even if the species is going to suffer from a global range reduction of up to 21 % under a pessimistic CO<sub>2</sub> emission scenario, very large areas will still present suitable climatic conditions for this highly problematic invasive species.

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Bioclimatic variables (source: Worldclim dataset)	
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Température Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Fig. S1

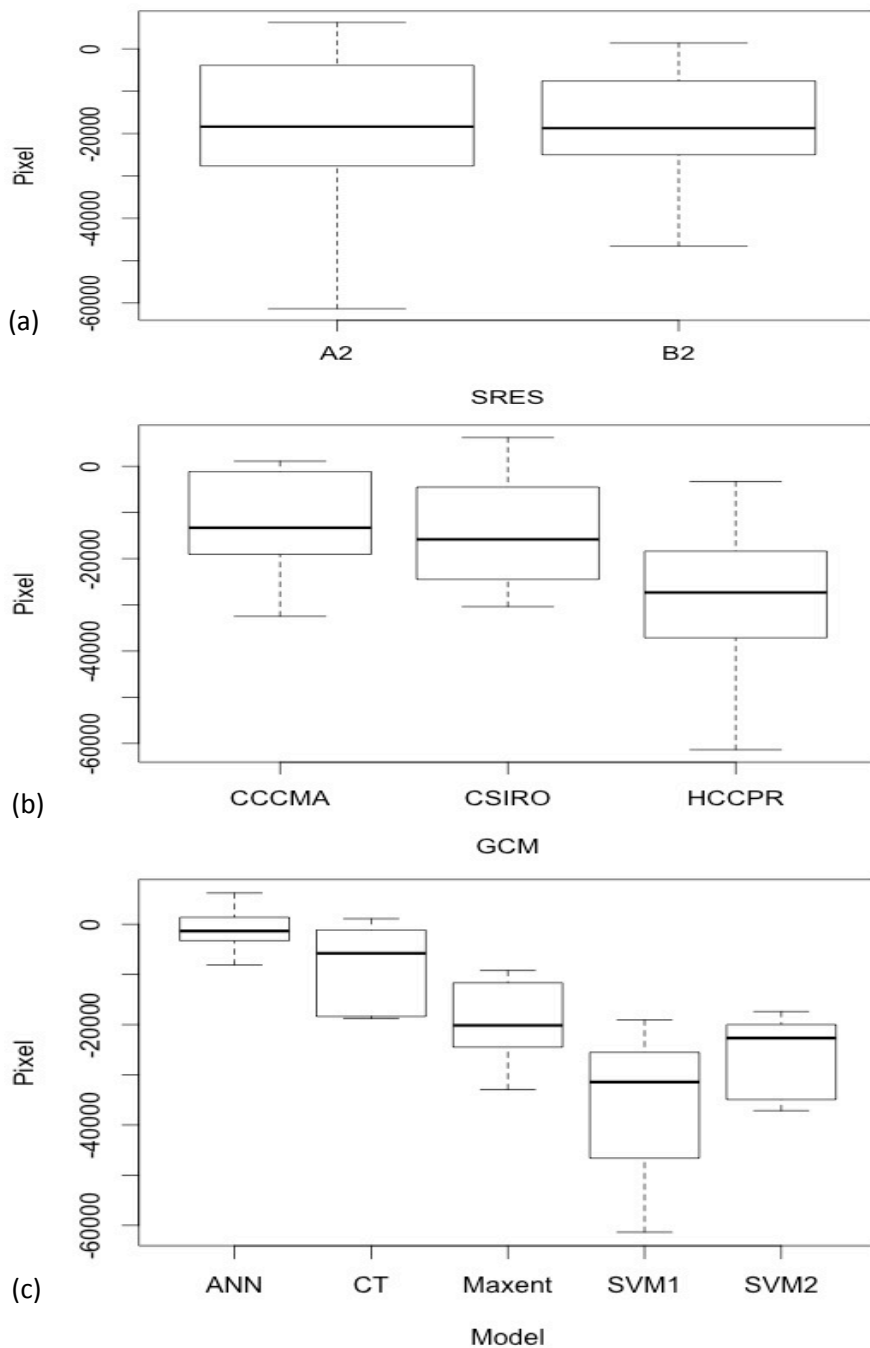


Fig S2. One-way ANOVA using raw data (change in pixel in 2080) to compare differences in individual model forecasts due to differences in (a) CO<sub>2</sub> emission scenarios (SRES), (b) climate models (GCM) and (c) modelling methods. There was no significant difference between projections under different CO<sub>2</sub> emission scenarios [ $F_{(1,28)}=0,01$ ,  $p=0,945$ ]. The difference between projections based on different GCMs [ $F_{(2,27)}=3,87$ ,  $p=0,033$ ] and different modelling methods [ $F_{(4,25)}=12$ ,  $p<0,001$ ] were significant, but all individual models were showing the same trend . The analysis was conducted using R software version 2.12.2.

Article title: Global warming may freeze the invasion of big-headed ants.

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# Worldwide Ant Invasions Under Climate Change

Cleo Bertelsmeier, Gloria M. Luque, Benjamin D.  
Hoffmann and Franck Courchamp





# 7. Worldwide ant invasions under climate change

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## *Abstract*

There is general consensus that the distributions of invasive species are likely to expand with climate change, however this dogma remains poorly tested. Here we model suitable area globally for 15 of the worst invasive ant species, both currently and with predicted climate change (in 2080), globally, regionally and within the world's 34 biodiversity hotspots. Surprisingly, the potential distribution of only five species was predicted to increase (up to 35.8%) with climate change, with most declining by up to 63.3%. The ant invasion hotspots are predominantly in tropical and subtropical regions of South America, Africa, Asia and Oceanic islands, and particularly correspond with biodiversity hotspots. Contrary to general expectations, climate change and invasive ant species will not systematically interact synergistically. However, ant invasions will likely remain as a major global problem, especially where invasion hotspots coincide with biodiversity hotspots.

**Keywords:** Biological invasions, species distribution models, climate change, invasive ants

## *Introduction*

Biological invasions are among the most important causes of the current biodiversity crisis (1), being involved in over half of the contemporary extinctions and the sole cause of one fifth of them (2). The number of exotic introductions has been rising steeply over the last century due to increased human-mediated transportation via tourism and commercial exchanges (3), and consequently the number of invasions is expected to increase exponentially (4).

Ants are very prominent as invasive species, with more than 200 species established outside their native range (5) and 19 being listed as highly problematic (6). In many instances ant invasions have caused the local decline and extinction of a variety of taxa, including arthropods, plants, birds, reptiles and mammals (7, 8). Economic losses can be high from decreased agricultural production, damage to infrastructure, and management expenses (9). For example, the red imported fire ant (*Solenopsis invicta*) alone is estimated to cost the US \$6 billion annually, and this cost is increasing (10). Some species can carry human diseases (11), and more than 200,000 people per year need medical treatment in the US alone from invasive ant stings (12).

There is a general, yet untested, consensus that climate change will exacerbate the threat posed by invasive species. This is especially so for ectotherms like ants whose current distributions are limited by thermal barriers (13–15). Surprisingly, few studies have

included climate change in their projections to test this assumption (16–19). Notably no global assessment predicting future ant invasions has been attempted. Yet, comparing global projections of the worst invasive ant species is crucial for identifying areas at most risk of invasion, and for implementing effective management responses. Here, we provide the first global risk evaluation for invasive ants following climate change using 15 of the most invasive ants.

The 15 species modelled here were all those with sufficient data among the 19 considered to be the most problematic by the Invasive Species Specialist Group (ISSG) of the International Union for the Conservation of Nature (IUCN). Of these species, five are in the list of the “100 of the world’s worst invasive species” (20): the big-headed ant (*Pheidole megacephala*), the little fire ant (*Wasmannia auropunctata*), the yellow crazy ant (*Anoplolepis gracilipes*), the Argentine ant (*Linepithema humile*) and the red imported fire ant (*S. invicta*). The remaining 10 species were the invasive garden ant (*Lasius neglectus*), the destroyer ant (*Monomorium destructor*), the flower ant (*Monomorium floricola*), the pharaoh ant (*Monomorium pharaonis*), the European fire ant (*Myrmica rubra*), the long-horned ant (*Paratrechina longicornis*), the tropical fire ant (*Solenopsis geminata*), the black imported fire ant (*Solenopsis richteri*), the white-footed ant (*Technomyrmex albipes*) and the ghost ant (*Tapinoma melanocephalum*).

We modelled the potential distribution of these species with the present climate and with a consensus of six climate change predictions by 2080 (i) at the global scale, (ii) within six continental regions (North America, South America, Asia, Oceania, Europe and Africa), and (iii) within the world’s biodiversity hotspots: 34 regions of very high levels of endemism and vulnerability (21). We used species distribution models, which explain a species’ distribution from a set of climatic predictor variables. We created consensus models based on five different modelling techniques, three Global Circulation Models and two Special Report on CO<sub>2</sub> Emission Scenarios to include a wide range of possible future climatic conditions (see materials and methods). We then compared the change of suitable area over time, both globally and regionally. Quality assurance tests indicated that model performance was good to excellent for all of the species (Fig. S1).

## Materials and Methods

### Species distribution data

Species distribution models search for a non-random association between environmental predictors and species occurrence data to make spatial predictions of suitable area. This method is based on the assumption that the species’ niche remains unchanged when extrapolations are made in space (new potential distribution) and time (future climate scenarios). However, we acknowledge that for invasive species in novel environments niche shifts can occur through genetic bottlenecks or rapid evolution leading to an invasive niche that differs from the native niche (33–35). Models based on only native range data often under-represent the potential invasive distribution, and these errors propagate when estimating climate change impacts (35, 36). Therefore we included occurrence points from both the invaded and native ranges to include the full set of climatic conditions under which each species can persist.

Data were sourced from the globally authoritative IUCN database for invasive species (6) as well as a database for ant distributions (37). We obtained additional points from two occurrence databases for *M. destructor* (38) and *L. neglectus* (39). All data points came from specimens that had been collected during the second half of the 20<sup>th</sup> century. Data were excluded where the species were present in artificial climatic conditions, such as greenhouses. One species, *T. albipes*, has had such a history of chronic mis-identification, that no data on any database can be considered to be reliable. Instead only we used location data of specimens inspected in the most recent taxonomic review of this genus (40). We used on average 237 points of occurrence to model each species' distribution (369 points of occurrence for *A. gracilipes*, 519 for *L. humile*, 153 for *L. neglectus*, 116 for *M. destructor*, 228 for *M. floricola*, 112 for *M. pharaonis*, 123 for *M. rubra*, 476 for *P. longicornis*, 208 for *P. megacephala*, 443 for *S. geminata*, 88 for *S. invicta*, 66 for *S. richteri*, 60 for *T. albipes*, 335 for *T. melanocephalum* and 261 for *W. auropunctata*). For models requiring absence data, 10,000 pseudo-absence (background) points were generated randomly throughout the world. The use of random pseudo-absence points is a standard procedure because confirmed absence data is difficult to obtain for most species and inherently impossible to prove (41).

#### *Climatic predictors*

We used 19 bioclimatic variables provided by the Worldclim database (42) to model each species' niche. We selected six variables that were not collinear (pair-wise  $r_{\text{Pearson}} < 0.75$ ) (Table. S1) and provided the greatest contribution to the Maxent model. These variable are frequently used in studies on climatic niches of species and impacts of climate change on species distributions because they are biologically meaningful (43). The bioclimatic variables were derived from monthly temperature and rainfall values from 1960-1990 (42), and represent annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperatures of the coldest and warmest month, and precipitations of the wet and dry quarters) (42) which are known to influence species distributions (44). We used a spatial resolution of 10 arcmin (approx. 18.5x18.5 km pixel).

Future climatic data were sourced from the 4<sup>th</sup> IPCC assessment report (45). The projections had been calibrated and statistically downscaled using the WorldClim data for 'current' conditions and therefore the projections could be compared. To consider a range of possible future climates, we used downscaled climate data from three Global Circulation Models (GCMs): the CCCMA-GCM2 model; the CSIRO-MK2 model; and the HCCPR-HADCM3 model (45). Similarly, we used the two extreme Special Report on CO<sub>2</sub> Emission Scenarios (SRES): the optimistic B2a; and pessimistic A2a scenario.

#### *Species Distribution Modelling*

Five machine learning modelling techniques were used to generate the consensual forecasts. Machine learning methods are among the most recently developed tools especially designed for prediction (46) and it has been claimed that their predictive performance exceeds that of more conventional techniques (47). The first two models were based on Support Vector Machines (SVM), which are a new generation of learning

algorithms (48). Recently, one-class SVMs have also been developed (41). We included a one-class SVM (parameters: kernel=Radial Base function,  $\gamma=1$ ,  $\nu=0.05$ ) in addition to the two-class SVM (parameters: type=C\_SVC, kernel= Radial Base function,  $\gamma=3$ , Cost=1). The third modelling algorithm that we used were Artificial Neural Networks (ANN) (parameters: type= Backpropagation ANN, Momentum=0.3, Learning rate=0.1) that have been successfully used to predict species distributions (41, 49). We also used Classification Trees (CT) (parameters: type= iterative, Number of trials=5, Window size=10, Pruning level=0.25), which partition the response variable into increasingly pure binary subsets with splits and stop criteria (50). The result was an average across 10 Classification Trees iterations of the model algorithm. Finally, we used the Maximum entropy method (Maxent), which has been widely used for distribution models for invasive species and impacts of climate change (51–54) (for a more detailed description of these algorithms see 19). All models were run using the ModEco Platform with default parameters (55).

A clear limitation of modelling is that outputs are dependent on the specifically chosen input data (56), in this instance the algorithms, global climate models and scenarios of human development. To minimise potential resultant variation we conducted consensus forecasts (57) of combined models using the five different modelling techniques with each of the three climate models (GCMs) with two CO<sub>2</sub> emission scenarios (SRES). The principle of consensus forecasts is to separate the signal from the “noise” associated with the errors and uncertainties of individual models, by superposing the maps based on individual model outputs. Areas where these individual maps overlap, are defined as areas of “consensus prediction” (57). This is different from averaging the individual projections, as the area predicted by the consensus forecast can be smaller than any individual forecast if there is little spatial overlap among individual forecasts. Simple averaging across individual forecasts is considered unlikely to match reality because averaging doesn’t take into account the spatial dimension of the forecast (57).

The contribution of individual models (i.e., the spatial prediction of “suitable range”) was weighted according to their AUC in order to enhance contribution of models with higher model performance values (23). Only binary projections (presence/absence) have been combined to generate the consensus model because continuous outputs can have different meanings for different models and cannot be simply added together (55). The combination of the individual forecasts then yields a projection (the consensus model), where the value of pixels vary between 0 and 1 and can be interpreted as a probability of the species being present in each pixel (57).

Consensus models were generated for the current climate (consensus across models using the five modelling techniques), and for six future climatic scenarios (3 GCMs x 2 SRES). A total climate change forecast model was also generated, including all six climatic scenarios (i.e., 30 individual projections, each based on a different combination of CO<sub>2</sub> scenario x GCM x modelling technique). This yielded a consensus projection for one particular point in time. We also calculated the standard deviation between climatic scenarios in order to show the extent of variation across forecasts (58) (Fig. S4).

Assessing suitable area

We applied a threshold rule whereby all pixels with a probability of presence exceeding 0.5 were classified as “suitable” area (41). By convention, this threshold is frequently used for binary classification for species distribution modelling (41, 59). Importantly, we did not intend to make projections with a certain a priori objective, but for studies with such objectives, the use of a range of different threshold values might be used (60). Spatial analyses were conducted using DIVA-GIS (61) and ArcGIS v 9.3.

We generated “invasion hotspot” maps by stacking the binary maps (species presence/absence) of the 15 species. This invasion hotspot map was superposed with a map of the biodiversity hotspots (21). We also created “shift” maps for the 15 species where we mapped predicted range gains losses and stability from the current to future climatic conditions. Finally, we calculated two indices to evaluate the extent of spatial shift: a “spatial congruence index” ( $2a/2a+b+c$ ) based on the Dice Sorensen dissimilarity measure and the “stable range” ( $a/(a+b)$ ) which is a measure of spatial shift versus stability (62), whereby: a = area suitable currently and in the future; b = area suitable currently only; c = area suitable in the future only

#### Model validation

Model robustness was evaluated using the Area Under the Curve (AUC) of the Receiver Operating Characteristic curve (see Fig. S1), which is a nonparametric threshold-independent measure of accuracy commonly used to evaluate species distribution models (e.g., 22, 23, 33). We used the AUC because it does not depend on the selected classification threshold, and it readily indicates if a model correctly discriminates between presence and absence points (53, 63). AUC values range from 0 to 1, where a value of 0.5 can be interpreted as a random prediction. AUC values between 0.5 and 0.7 are considered low (poor model performance), 0.7 – 0.9 moderate and >0.9 high ((41) and references therein). For model evaluation, the data needs to be split into a train and a test group. We used 10-fold cross-validation, whereby the data was split into 10 equal parts, with 9/10 of the observations used to build the models and the remaining 1/10 used to estimate performance. This was repeated ten times and the estimated performance measures were averaged (41, 64).

#### Results

Under current climatic conditions, on average 15% of terrestrial land was found to be climatically suitable for the 15 invasive ants, with potential distributions ranging from 21.1% of the global surface for *M. destructor* to only 3% for *S. richteri* (Fig. S2). The continental regions differed greatly in their susceptibility to ant invasions, even for species with sympatric native ranges, such as *S. invicta* and *L. humile*. For example, large areas of Europe were suitable for three species (*L. humile*, *L. neglectus* and *M. rubra*) but Europe was barely suitable (<2%) for the remaining 12 species (Fig. 1). Conversely, much of Oceania was suitable for all except one species, varying from 4.6% to 44.4% (Fig. 1). Overall, the northern hemisphere had a relatively low proportion of suitable area for most species, whereas most of Oceania and South America was predicted to be suitable to almost all invasive ants (Fig. 2).

Contrary to expectations, suitable area increased with climate change only for five species (Fig. S3), ranging between +6.3% to +35.8%. Instead, it decreased for most (8: ranging between -64.3% and -2.6%) species and remained stable for the remaining two species. Of the five species within the “100 of the worst invasive species” list, four showed declines in suitable area worldwide. This indicates that invasive ants will not systematically benefit from climate change at a global scale, but rather follow the trend of biodiversity in general, which is predicted to decline with climate change (22). Patterns of potential range shifts also varied considerably (Fig. 3). Overlap between species’ current and future potential distributions ranged from 98.1% (*S. geminata*) to only 49.4% (*T. albipes*) (Fig. S4). The proportion of currently suitable area that remained suitable in 2080 varied between 33.7% (*T. albipes*) and 99.2% (*M. destructor*) (Fig. S4). The potential distribution of *S. invicta* increased in all regions, whereas that of *P. megacephala* decreased in all regions and the dynamics of all other species were non-uniform. Similarly, the patterns were heterogeneous within and among regions, being most consistent in Europe where no species were predicted to decrease, six would increase and nine would remain stable.

Strikingly, the average proportion of current suitable area of the biodiversity hotspots (39.5%) was 2.6 times greater than for the world overall (15%) (Fig. 4a). As the biodiversity hotspots are largely within tropical regions, they are highly suitable for most invasive ants, which are predominantly of tropical or subtropical origin. The amount of suitable area within the biodiversity hotspots was greatest for *P. megacephala* (61.8%), followed by *W. auropunctata* (61.3%), *M. pharaonis* (56.4%) and *T. albipes* (51.5%). When we superposed individual invasion predictions for the 15 species to create cumulative world maps of “invasion hotspots”, the invasion hotspots largely overlapped with the biodiversity hotspots (Fig. 2). Following climate change, the models predicted that the proportion of suitable areas within the biodiversity hotspots would increase for five species, *M. destructor* (+19.7%), *S. invicta* (+16.3%), *P. longicornis* (+8.5%), *S. geminata* (+7.4%) and *M. pharaonis* (+3.7%), and decrease or remain similar for the other species. The average proportion of suitable area of the hotspots (37%) remained much higher than for the rest of the world (14.6%) (Fig 4b).

### Discussion

Our models have shown that a large amount of global landmass is currently climatically suitable to invasive ants, especially in the biodiversity hotspots, where biodiversity is most unique and most vulnerable. Many areas are highly suitable for several invasive ants, which have clearly not yet reached their entire potential distribution (Fig. S2). However, contrary to general expectations, climate change will not result in range expansion for most species, and thus these two drivers of species extinction (climate change and invasive species) will not systematically interact synergistically (13, 14). The variability in responses to climate change (from an increase by +35.8% to a decrease by -63.3%) was especially surprising given that all species are from one family, the *Formicidae*, occur in similar habitats and have similar ecological characteristics (7, 12). Nevertheless, expansion is predicted for some species, and important spatial shifts are observed for most species. Consequently, ant invasions will likely remain as a major global problem, especially where invasion hotspots coincide with biodiversity hotspots.

A number of underlying assumptions and inherent uncertainties are associated with the niche modelling approach (23–26) and the actual distribution is contingent on many factors, including dispersal, biotic resistance and in particular disturbance (23–26). But regardless of whether or not invasive species have a greater impact or are better colonizers of disturbed habitats (27), suitable climate remains a prerequisite for the establishment of these invasive species in new regions of the world. Bioclimatic models are generally thought to deliver valuable approximations of potential distributions (28, 29) and the climate/habitat match is the only determinant that consistently and significantly explains invasion patterns across taxonomic groups (30).

As management of invasive ants is extremely difficult because of their small size and their colonial lifestyle, it is usually better to prevent invasions whenever possible than to control them later (31). Our models can help to target potential invasive species in advance to allow managers to be proactive. They also allow drawing special attention to high-risk species at ports of entry (32). Furthermore, managers can adjust priorities under changing environmental conditions such as climate change (14), which could favour some species or places over others.

Given the substantial damage caused by invasive ants to biodiversity, economies and human health, as well as the difficulty and cost managing invasions, predictive studies such as this will greatly improve our ability to take a proactive approach against this global threat.

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## Figure Legends

Fig. 1 Proportion of climatically suitable areas under current (light blue) and future (dark blue) climatic conditions within six continental regions. Ant species codes: Ag= *A. gracilipes*, Lh= *L. humile*, Ln= *L. neglectus*, Md= *M. destructor*, Mf= *M. floricola*, Mp= *M. pharaonis*, Mr= *M. rubra*, Pl= *P. longicornis*, Pm= *P. megacephala*, Sg= *S. geminata*, Si= *S. invicta*, Sr= *S. richteri*, Ta= *T. albipes*, Tm= *T. melanocephalum*, Wa= *W. auropunctata*.

Fig. 2. Map superposing the suitable areas of the 15 invasive ant species (binary presence-absence predictions) under current climatic conditions. The colour gradient indicates the number of invasive species with sympatric predicted distributions (from light purple=0 to very dark purple=11), thus very dark areas indicate “invasion hotspots”. The black lines delimit the 34 biodiversity hotspots. The pie charts show the proportion of areas suitable for 0 to 11 invasive species globally and within the biodiversity hotspots.

Fig. 3. Spatial shift of suitable areas of five ant species that demonstrate different patterns. Blue areas = only suitable under current climatic conditions; red areas = only suitable under

future climatic conditions (2080); and yellow areas = suitable under both current and future climatic conditions.

Fig. 4. Proportion of suitable areas under current climatic conditions globally (blue) and within the 34 biodiversity hotspots (green) for each of the 15 invasive ant species. Ant species codes as in Figure 1. (a) Projections under current climatic conditions, (b) projections in 2080.

### Supplementary figure legends

S1. Variation in model performances as determined by the area under the curve (AUC) of the Receiver Operating Characteristic curve, mean  $\pm$  sd) across the 5 algorithms for the 15 ant species. Ag= *A. gracilipes*, Lh= *L. humile*, Ln= *L. neglectus*, Md= *M. destructor*, Mf= *M. floricola*, Mp= *M. pharaonis*, Mr= *M. rubra*, Pl= *P. longicornis*, Pm= *P. megacephala*, Sg= *S. geminata*, Si= *S. invicta*, Sr= *S. richteri*, Ta= *T. albipes*, Tm= *T. melanocephalum*, Wa= *W. auropunctata*

S2 Maps of current and future (2080) climatic suitability for the 15 invasive ant species.

S3 Variation in predicted changes of suitable area between 6 future climatic scenarios (including 2 SRES and 3 GCMs) for the 15 invasive ant species. Red lines indicate the values of the consensus models. Ag= *A. gracilipes*, Lh= *L. humile*, Ln= *L. neglectus*, Md= *M. destructor*, Mf= *M. floricola*, Mp= *M. pharaonis*, Mr= *M. rubra*, Pl= *P. longicornis*, Pm= *P. megacephala*, Sg= *S. geminata*, Si= *S. invicta*, Sr= *S. richteri*, Ta= *T. albipes*, Tm= *T. melanocephalum*, Wa= *W. auropunctata*

S4 Spatial shift of net suitable area of the 15 invasive ant species. Areas in blue= only suitable under current climatic conditions; areas in red= only suitable under future (2080) climatic conditions; areas in yellow= suitable under both current and future climatic conditions.  $\sigma$ = Spatial congruence.  $\Upsilon$ = Stable range. Ag= *A. gracilipes*, Lh= *L. humile*, Ln= *L. neglectus*, Md= *M. destructor*, Mf= *M. floricola*, Mp= *M. pharaonis*, Mr= *M. rubra*, Pl= *P. longicornis*, Pm= *P. megacephala*, Sg= *S. geminata*, Si= *S. invicta*, Sr= *S. richteri*, Ta= *T. albipes*, Tm= *T. melanocephalum*, Wa= *W. auropunctata*

### Supplementary Table legends

Table S1 Non-collinear variables (see materials and methods), used to model each species' potential distribution (6 variables per species).

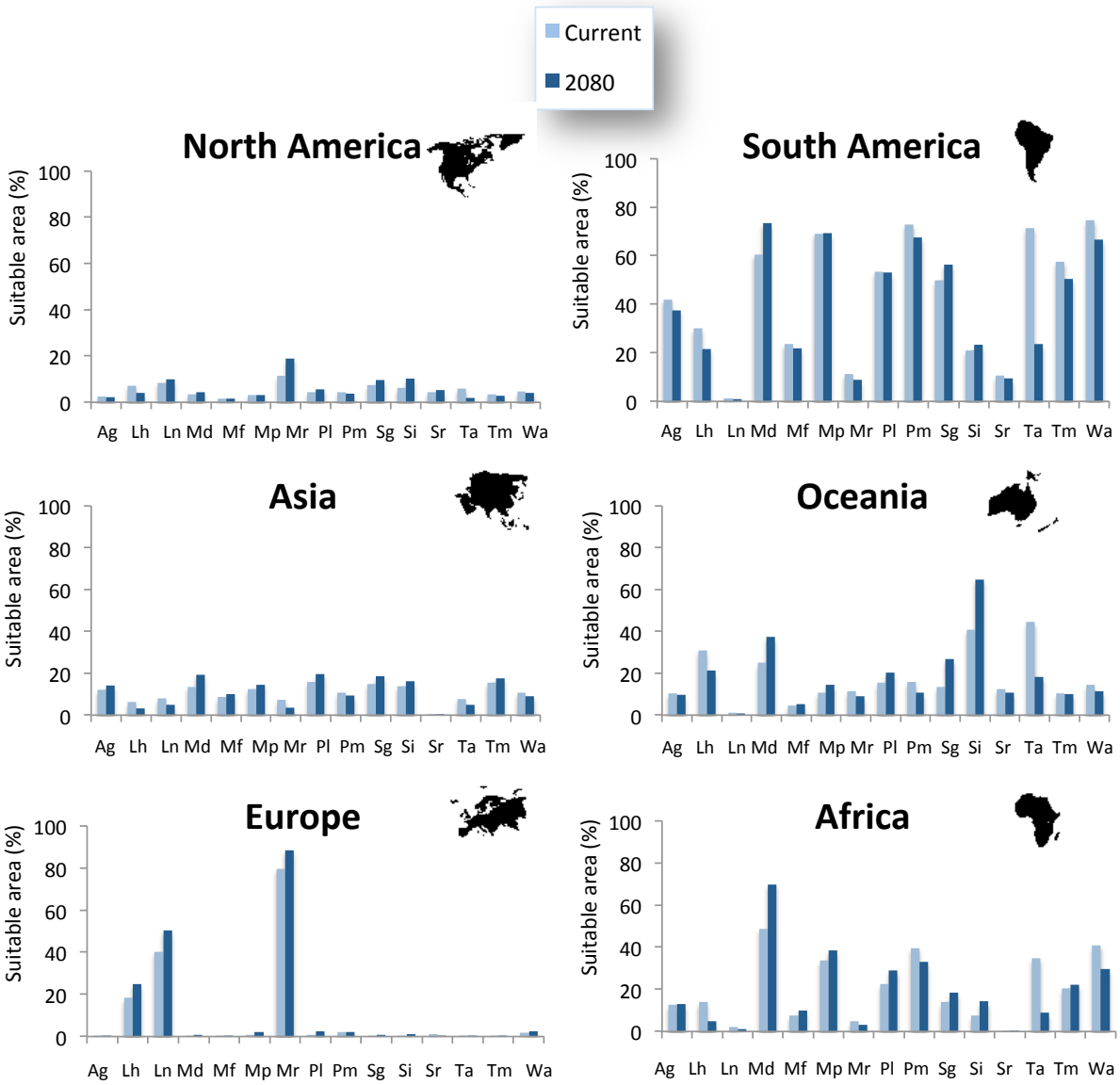


Fig. 1

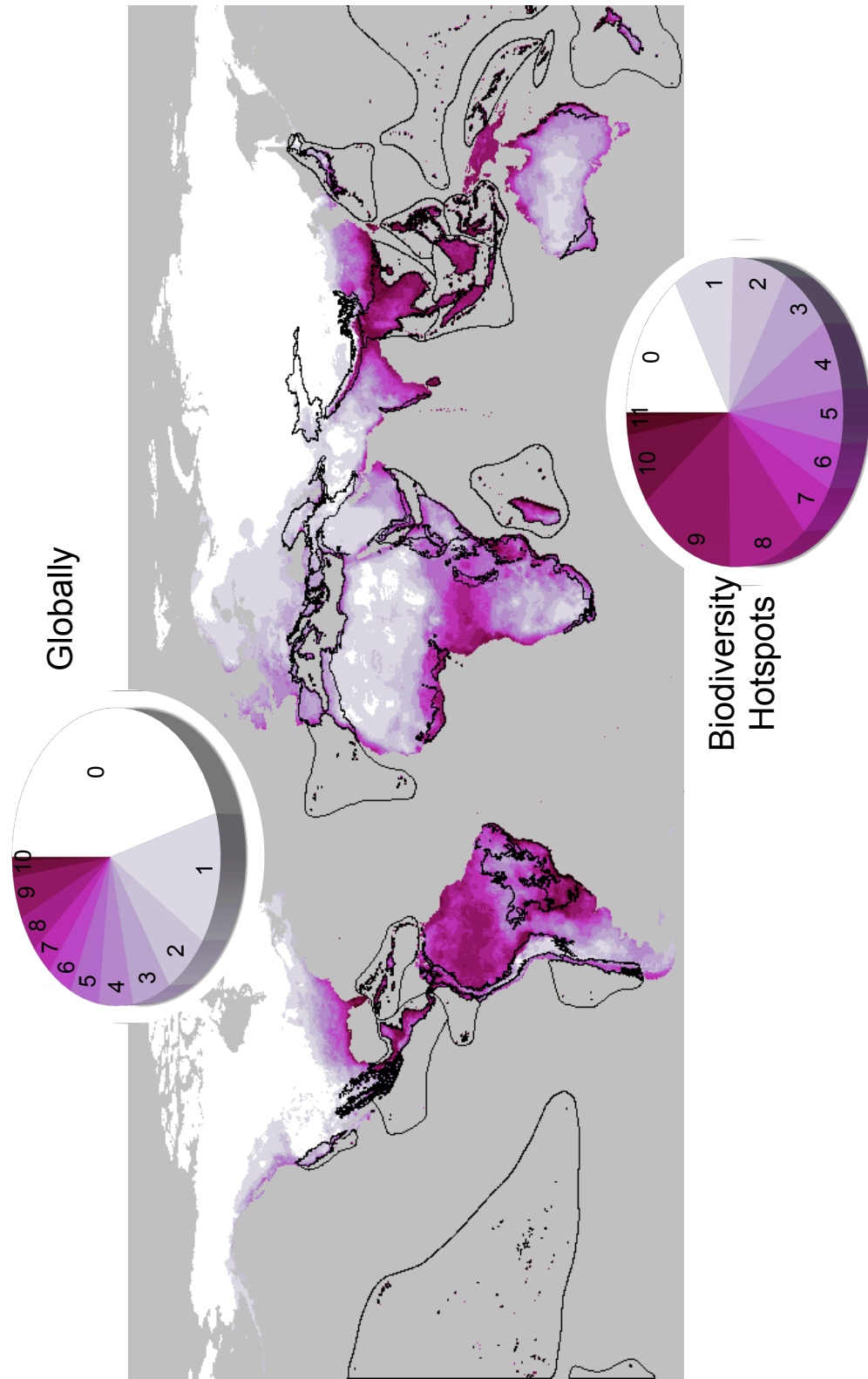


Fig. 2

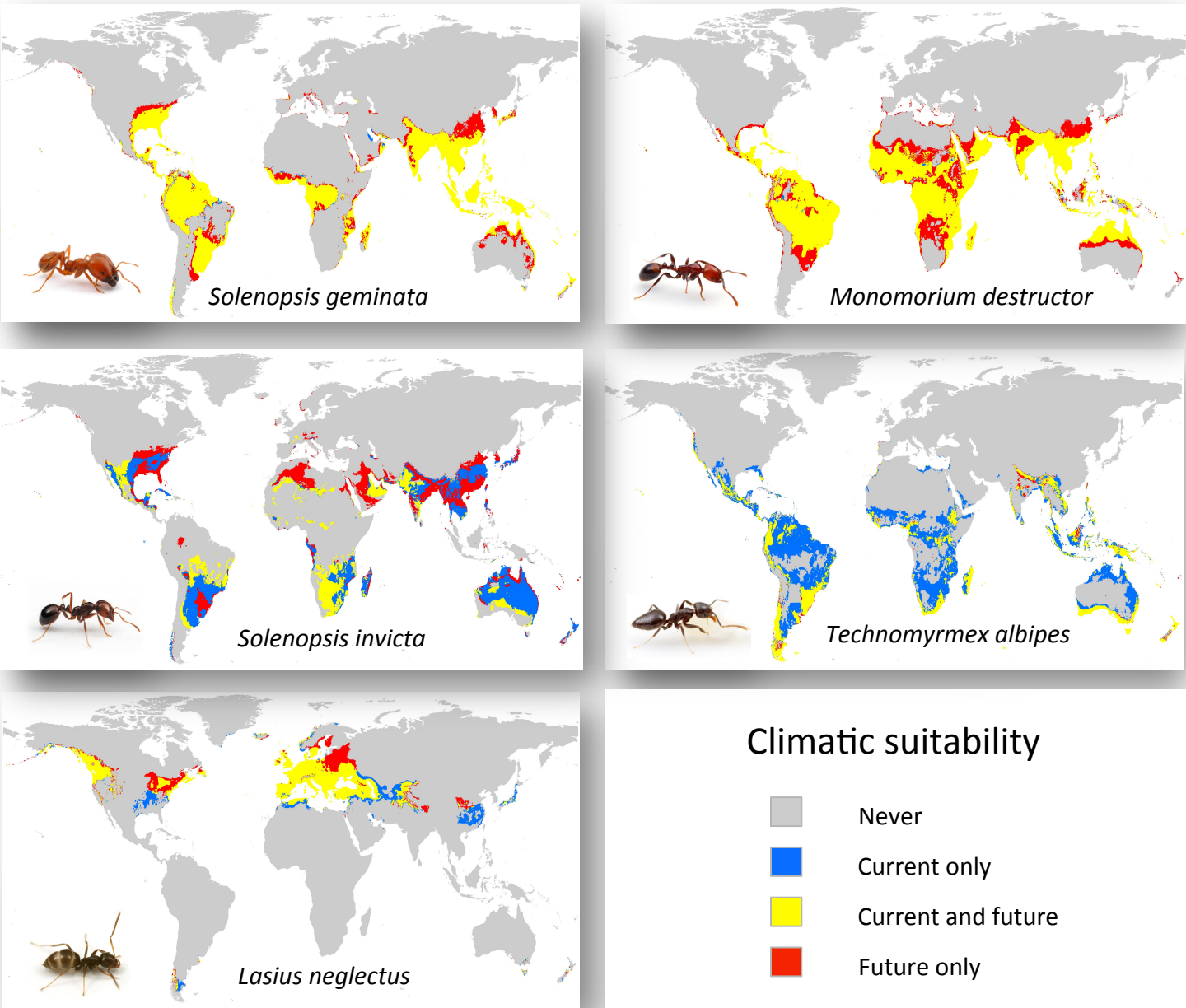
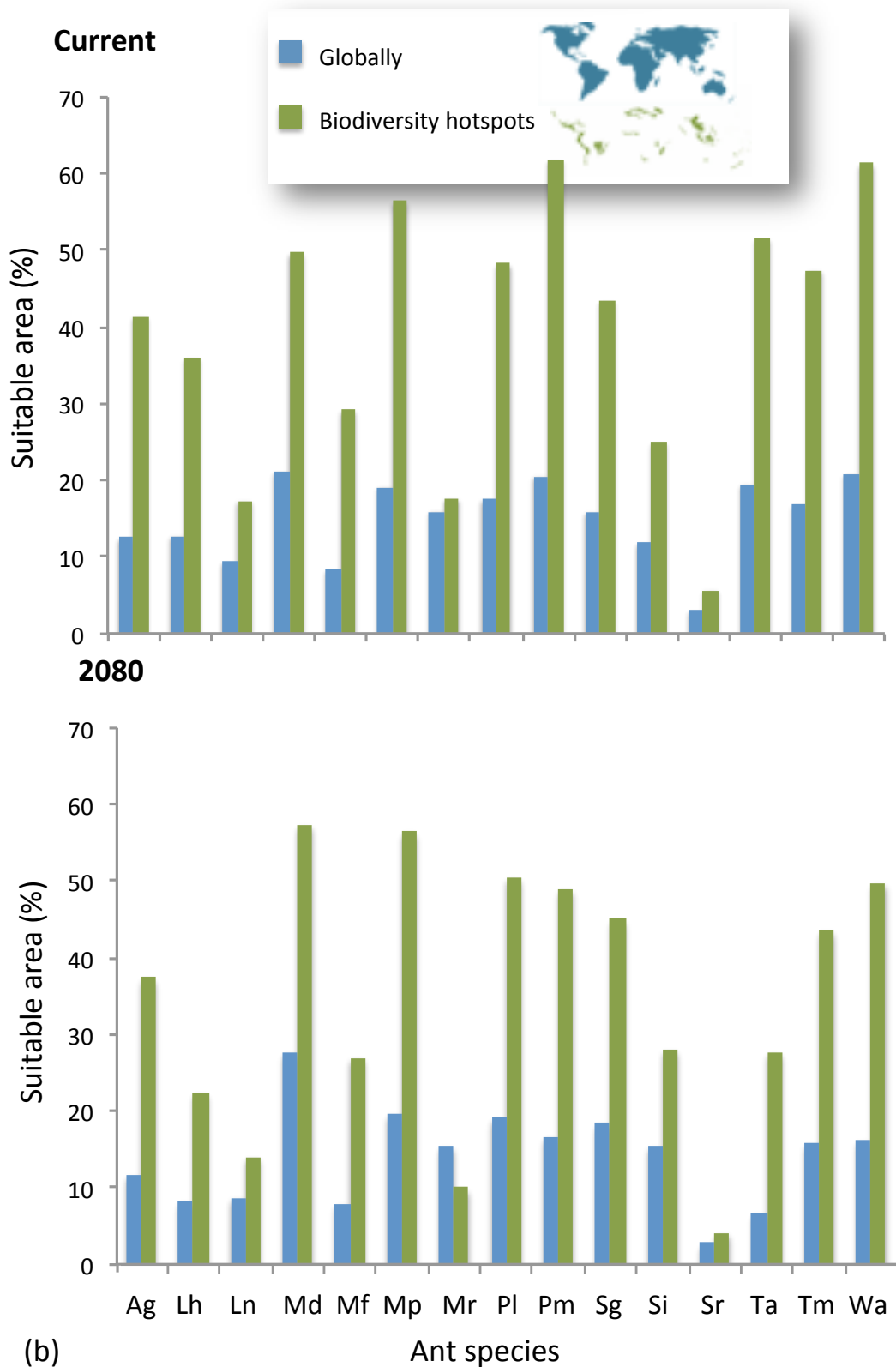


Fig. 3





(b)

Fig 4

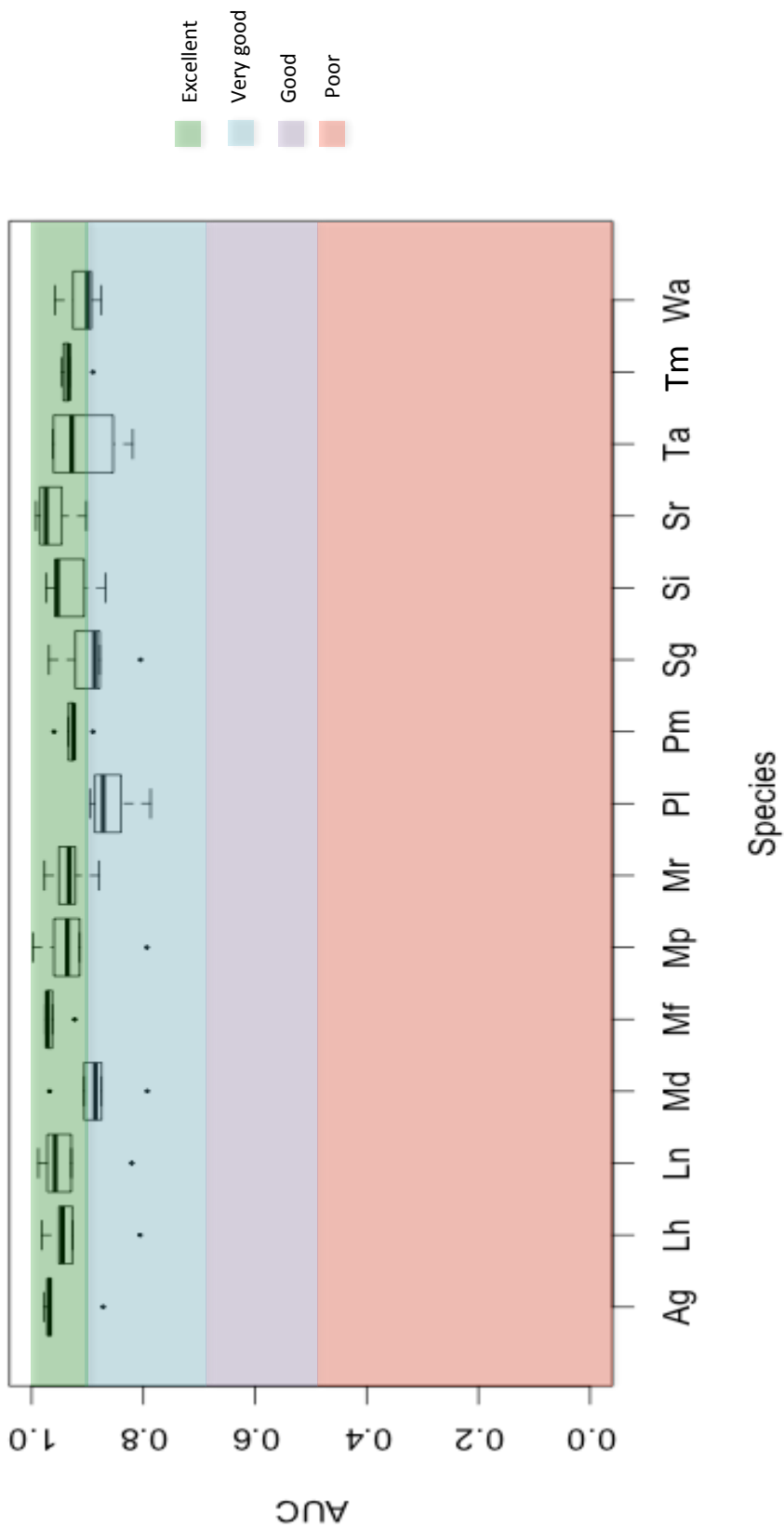
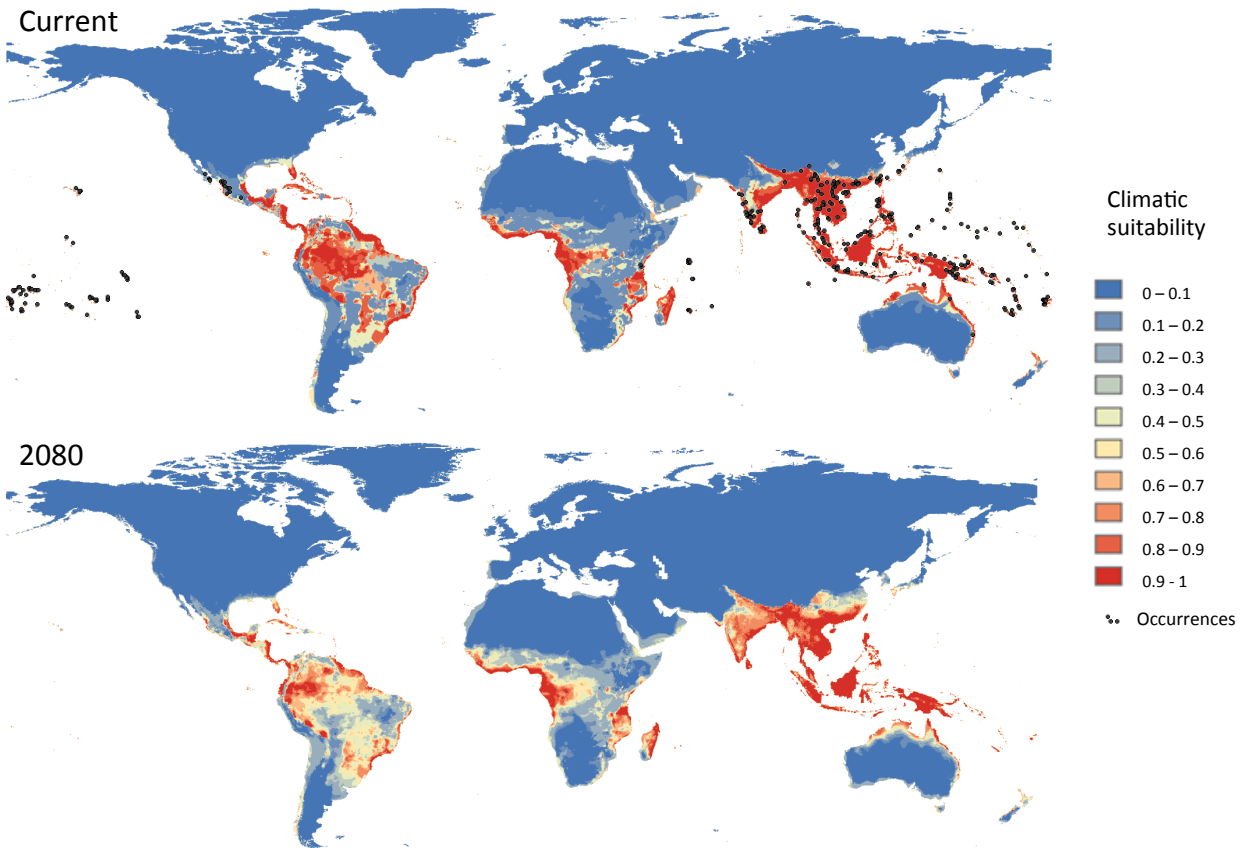


Fig. S1

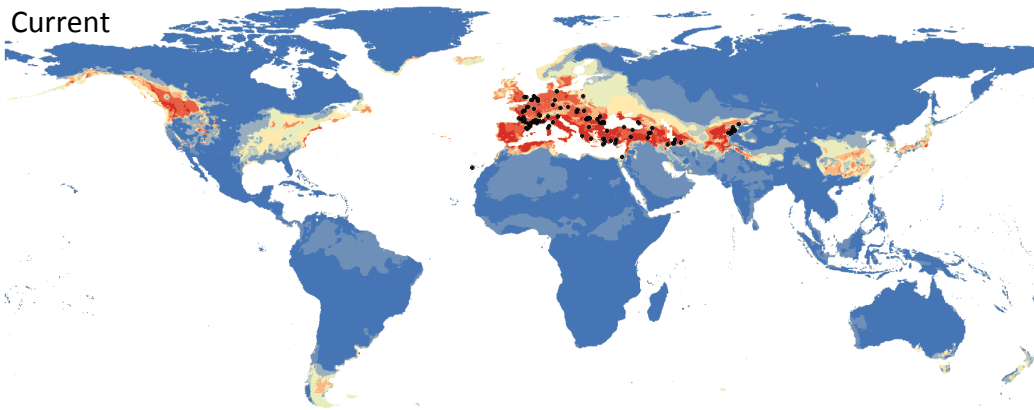
# Current and future (2080) potential distribution of 15 of the worst invasive ant species

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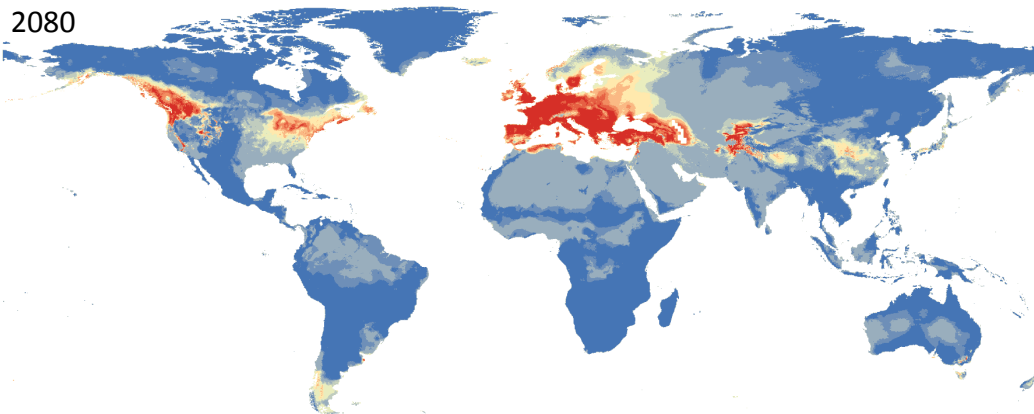


*Lasius neglectus*

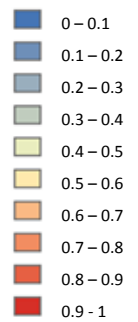
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2080



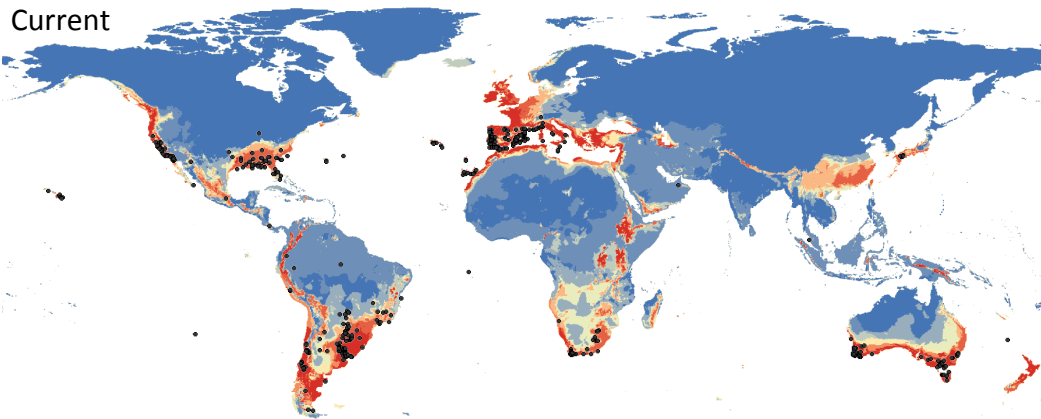
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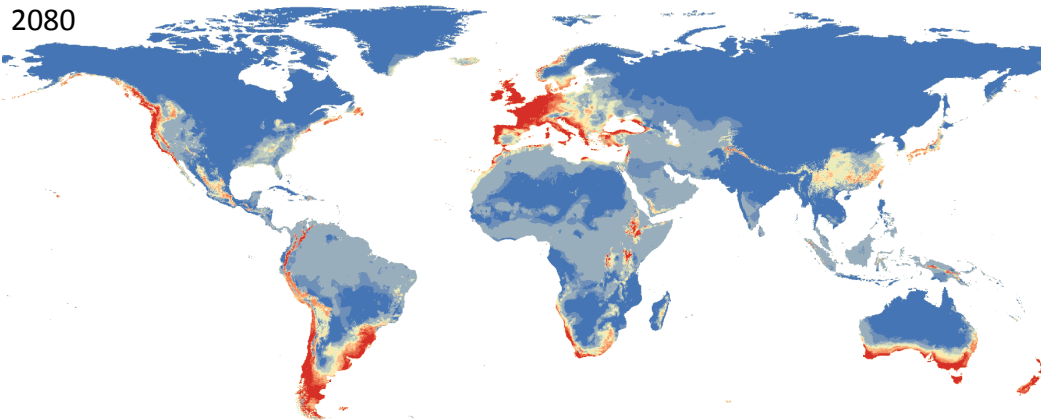
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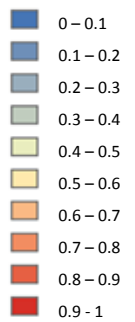
Current



2080



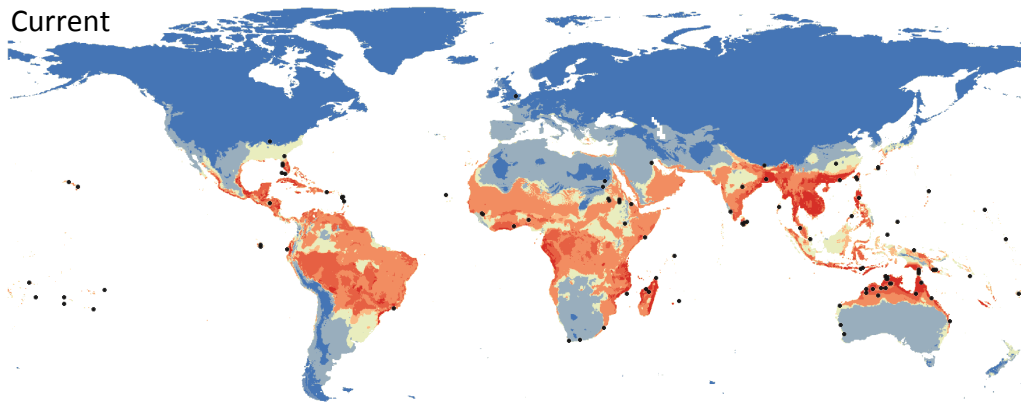
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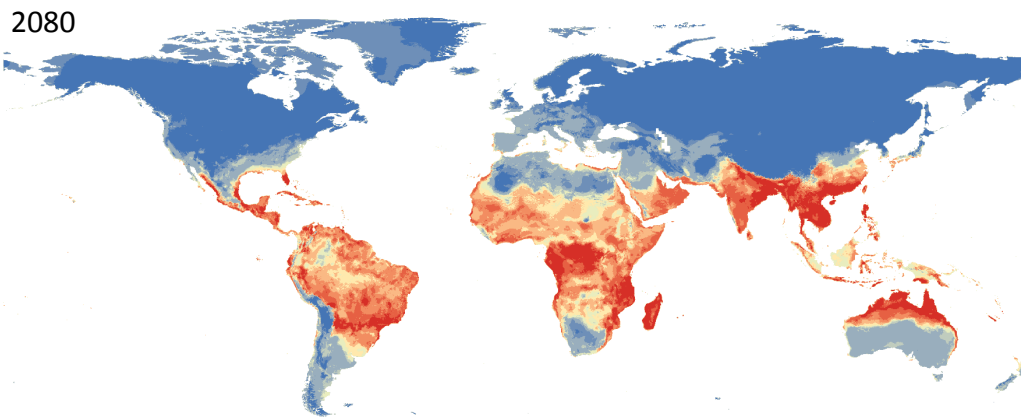
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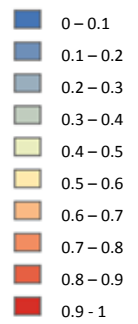
Current



2080



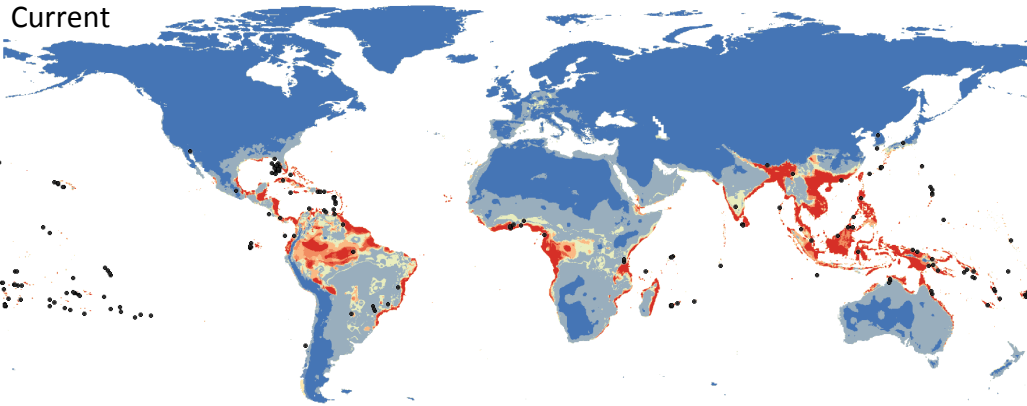
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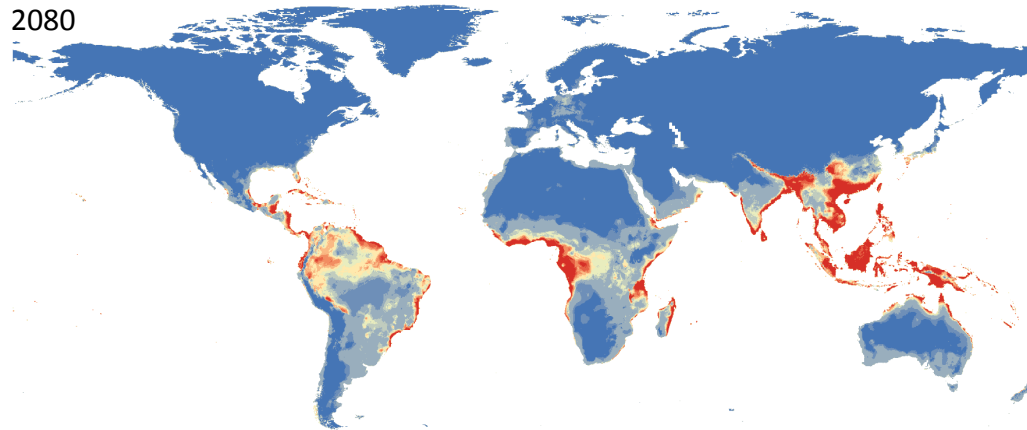
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*Monomorium floricola*

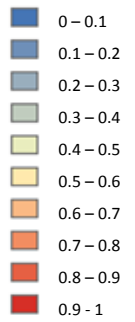
Current



2080



Climatic suitability

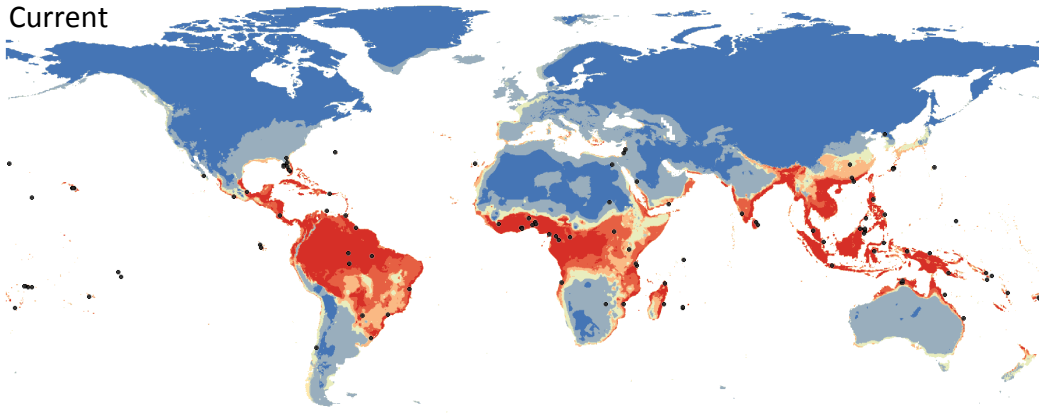


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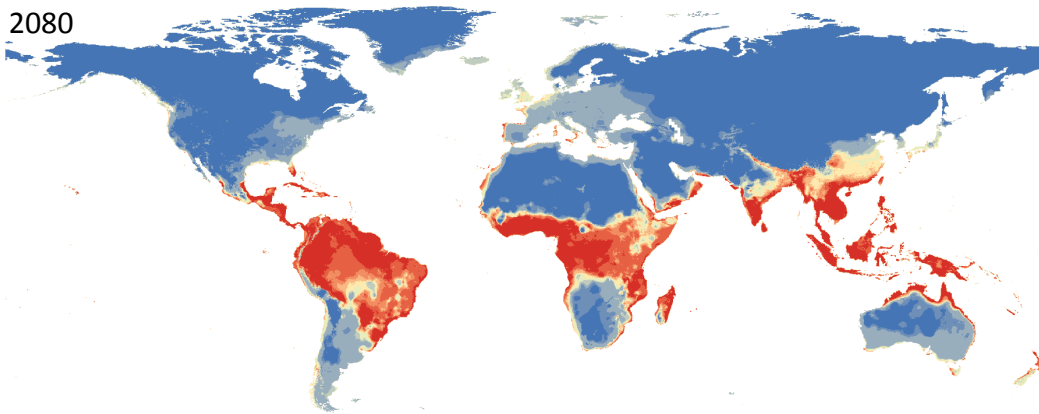


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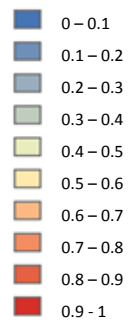
Current



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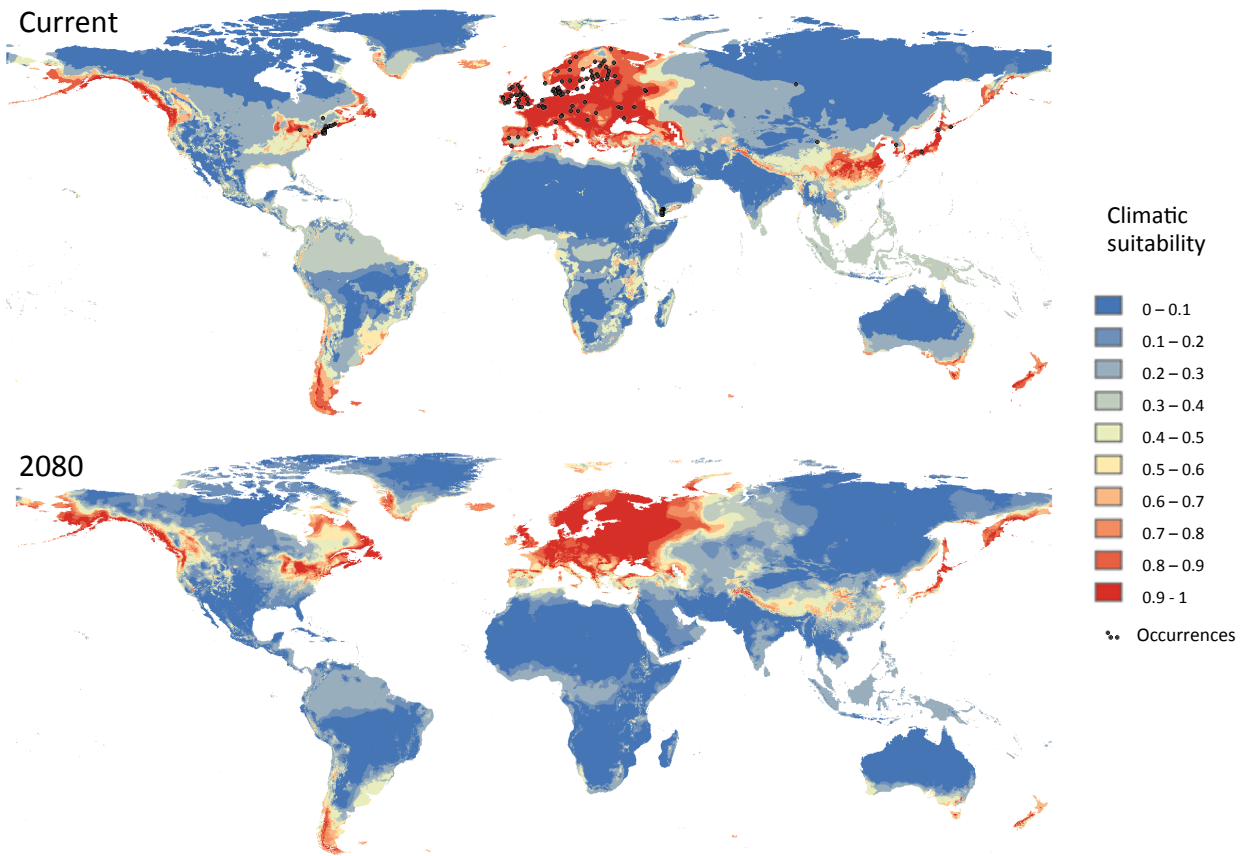


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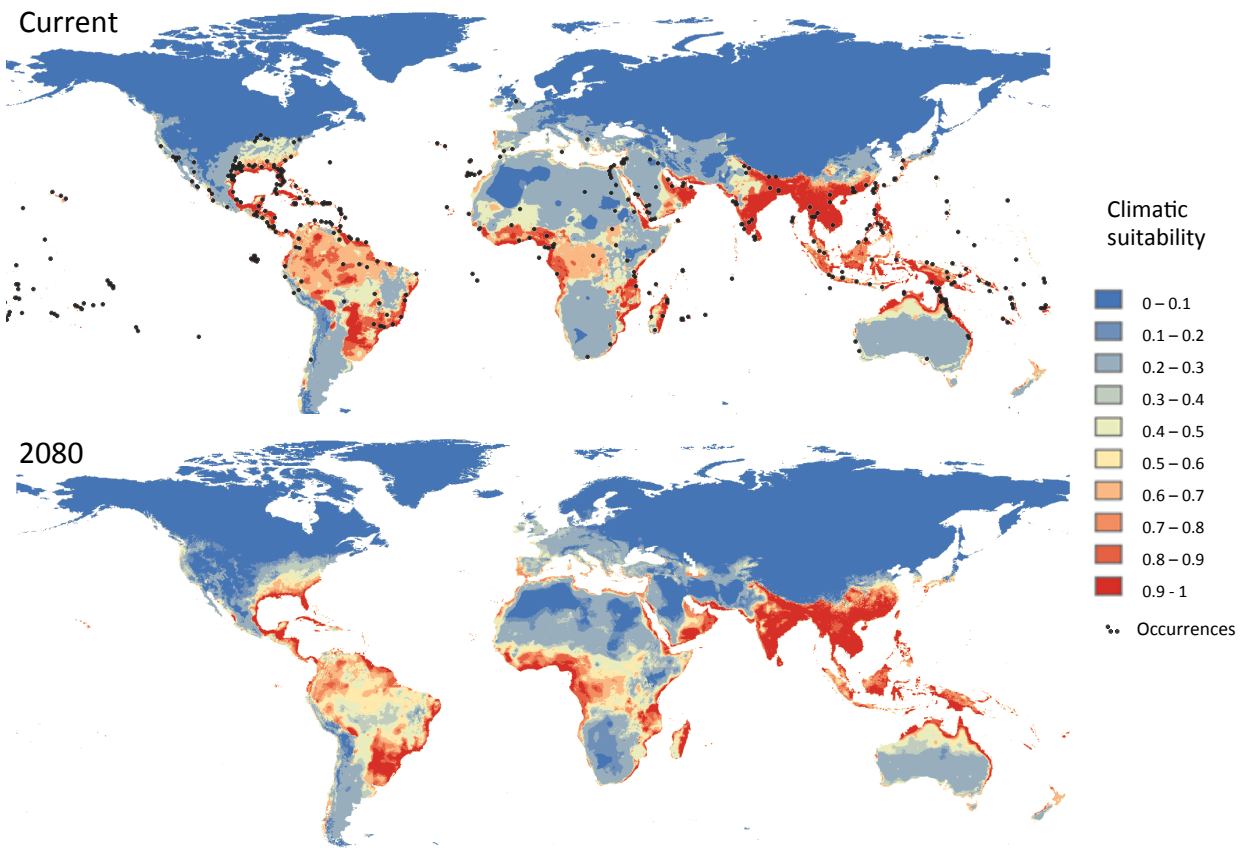


•• Occurrences

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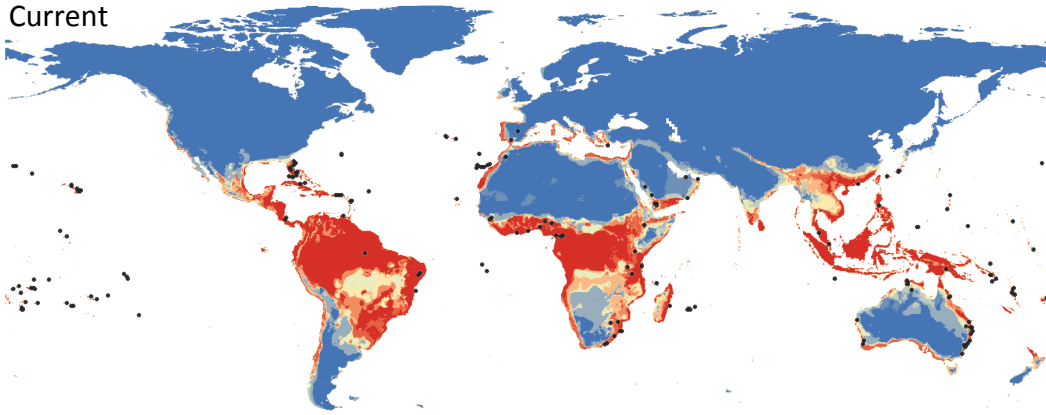


*Paratrechina longicornis*

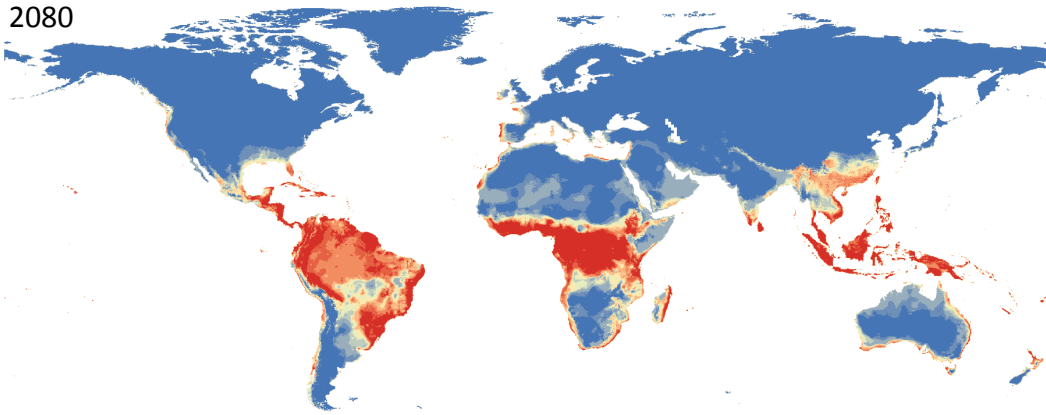


*Pheidole megacephala*

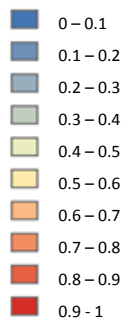
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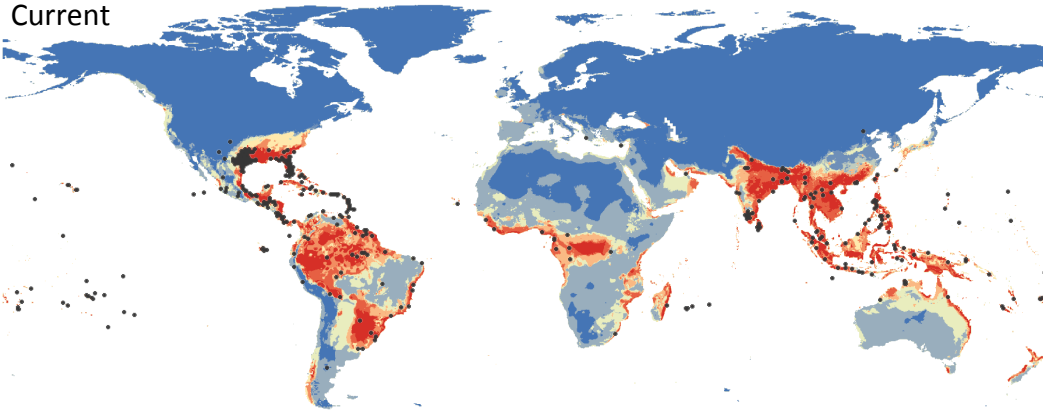
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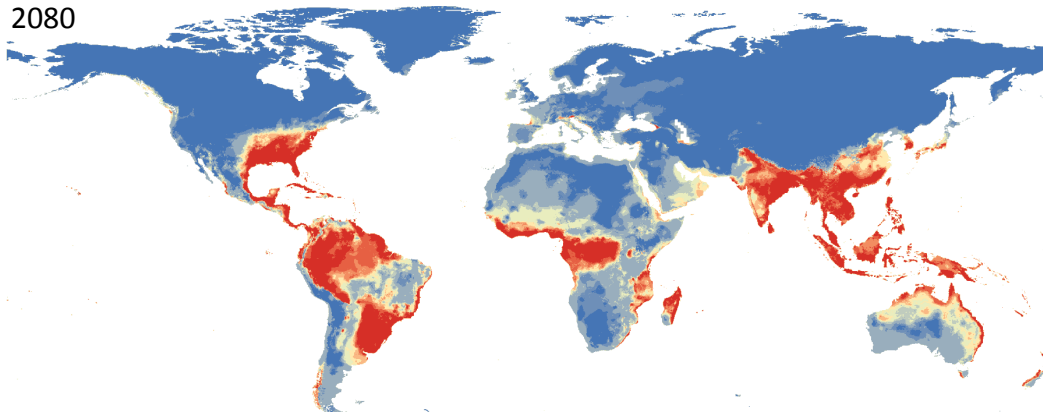
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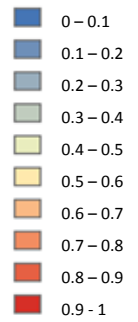
Current



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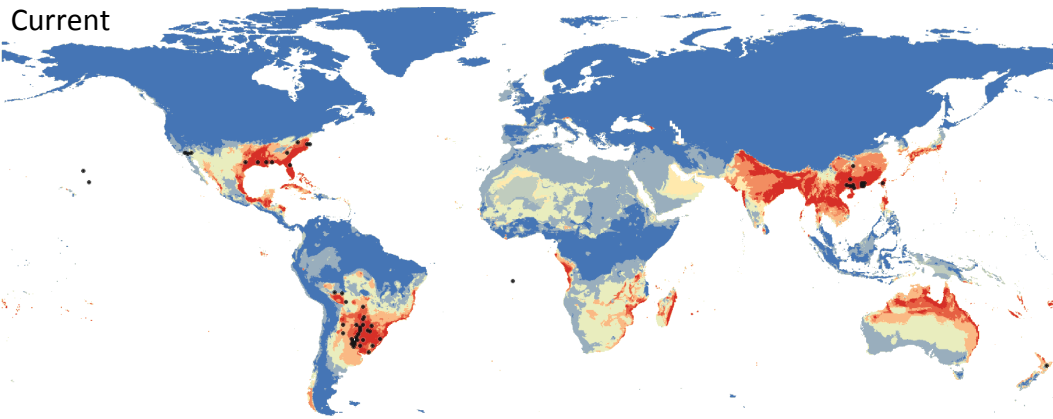
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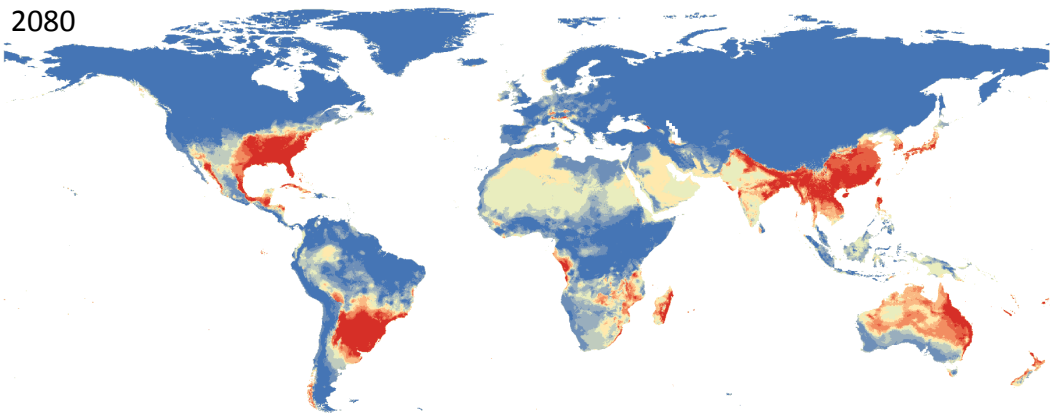
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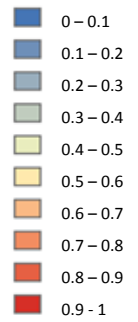
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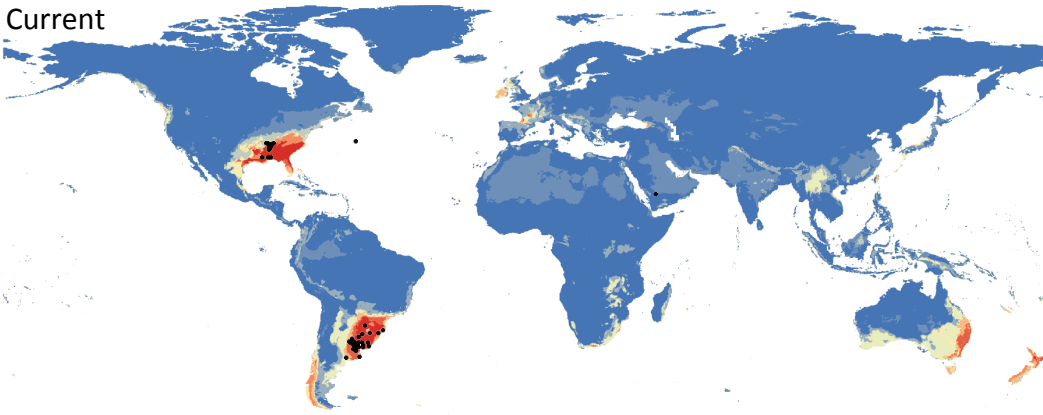
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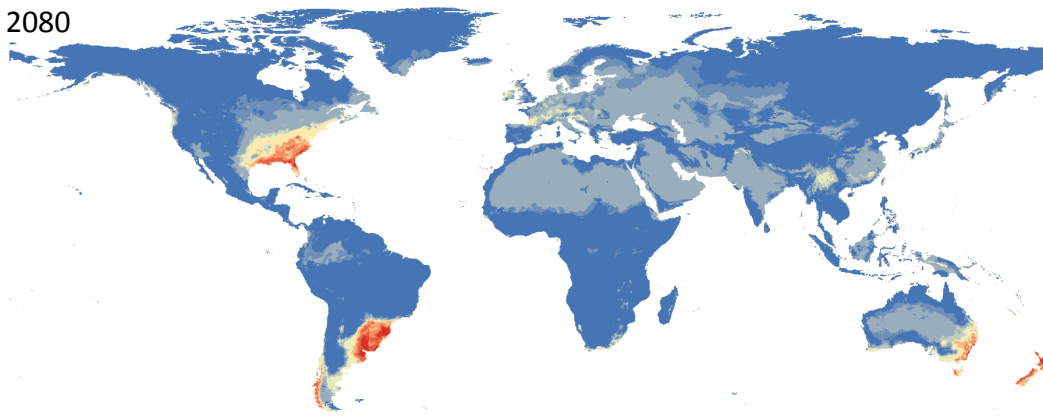
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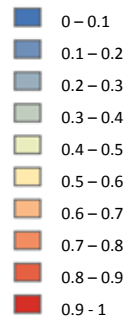
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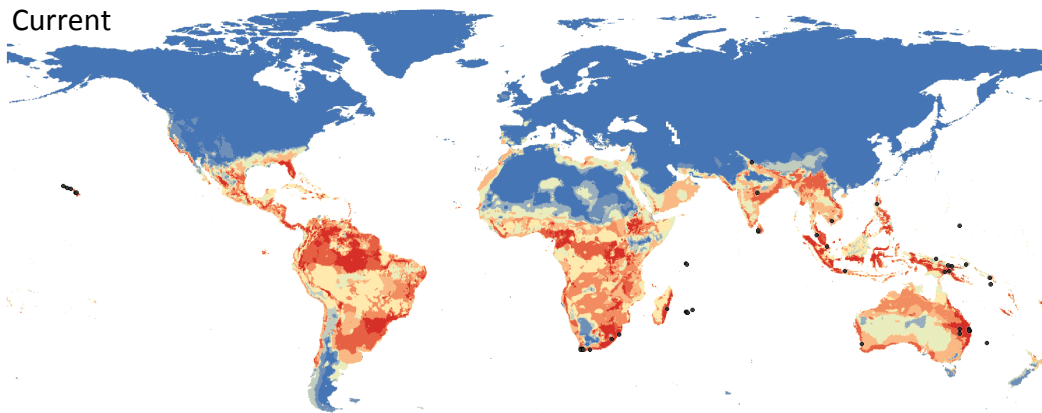
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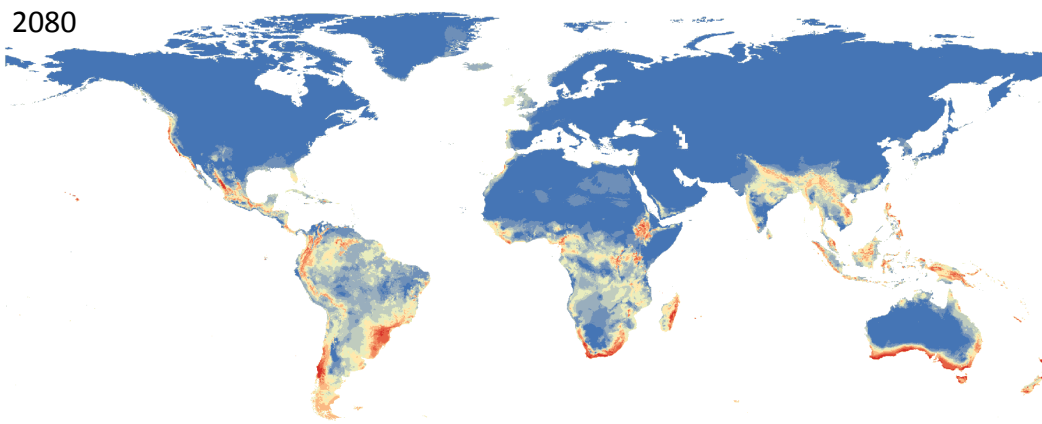
•• Occurrences

*Technomyrmex albipes*

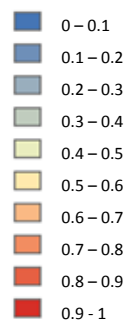
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Climatic suitability

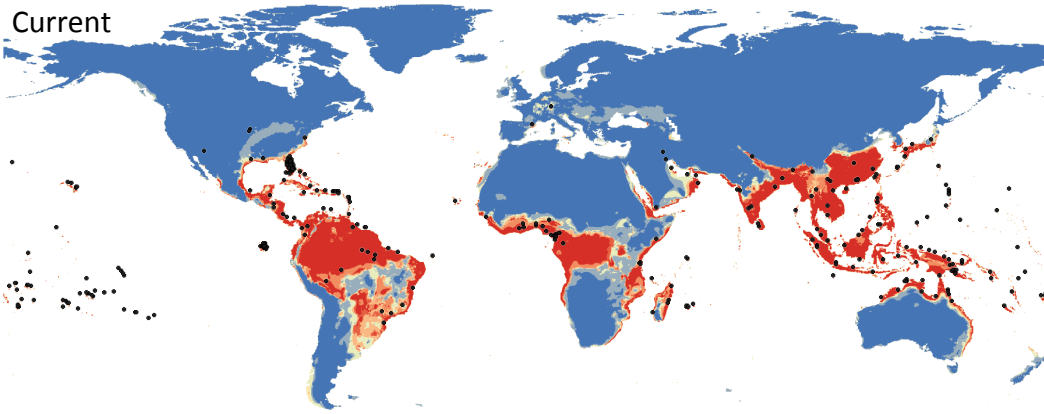


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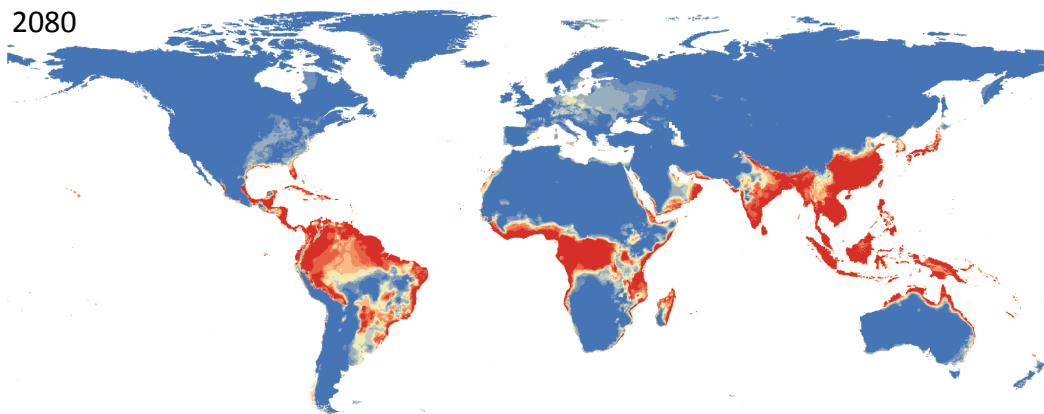


*Tapinoma melanocephalum*

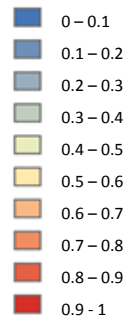
Current



2080



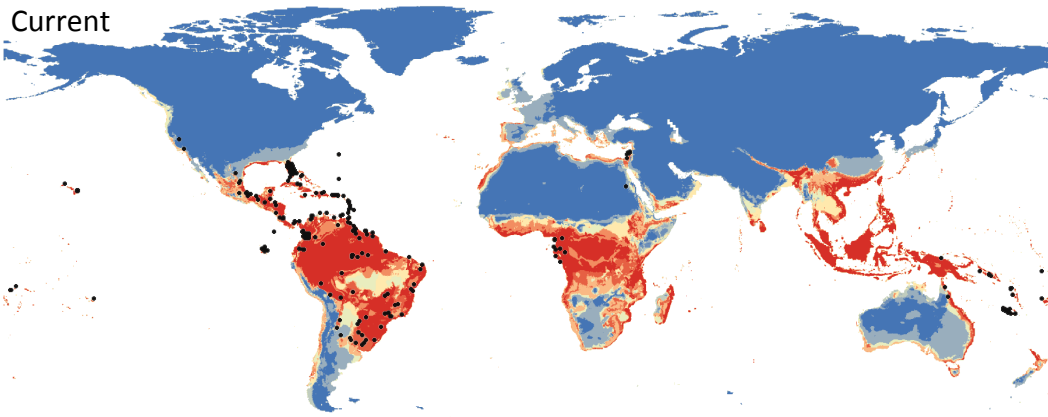
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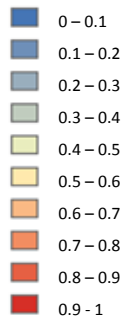
•• Occurrences

*Wasmannia auropunctata*

Current

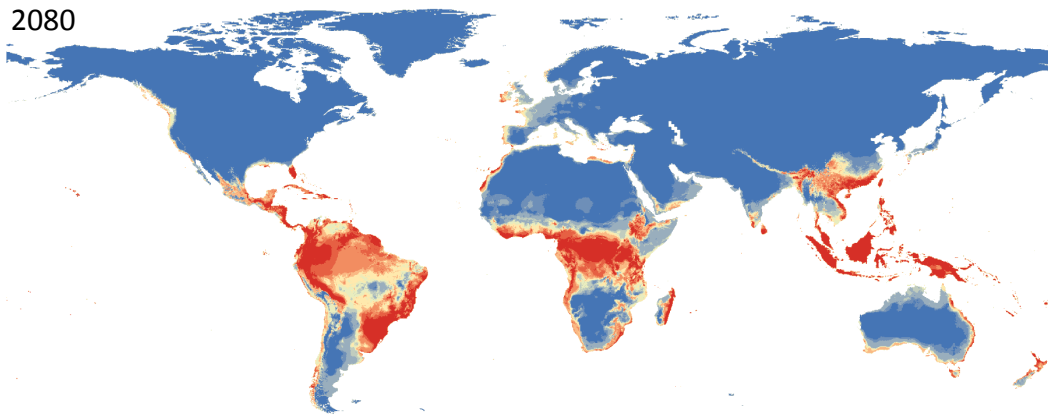


Climatic suitability



• Occurrences

2080



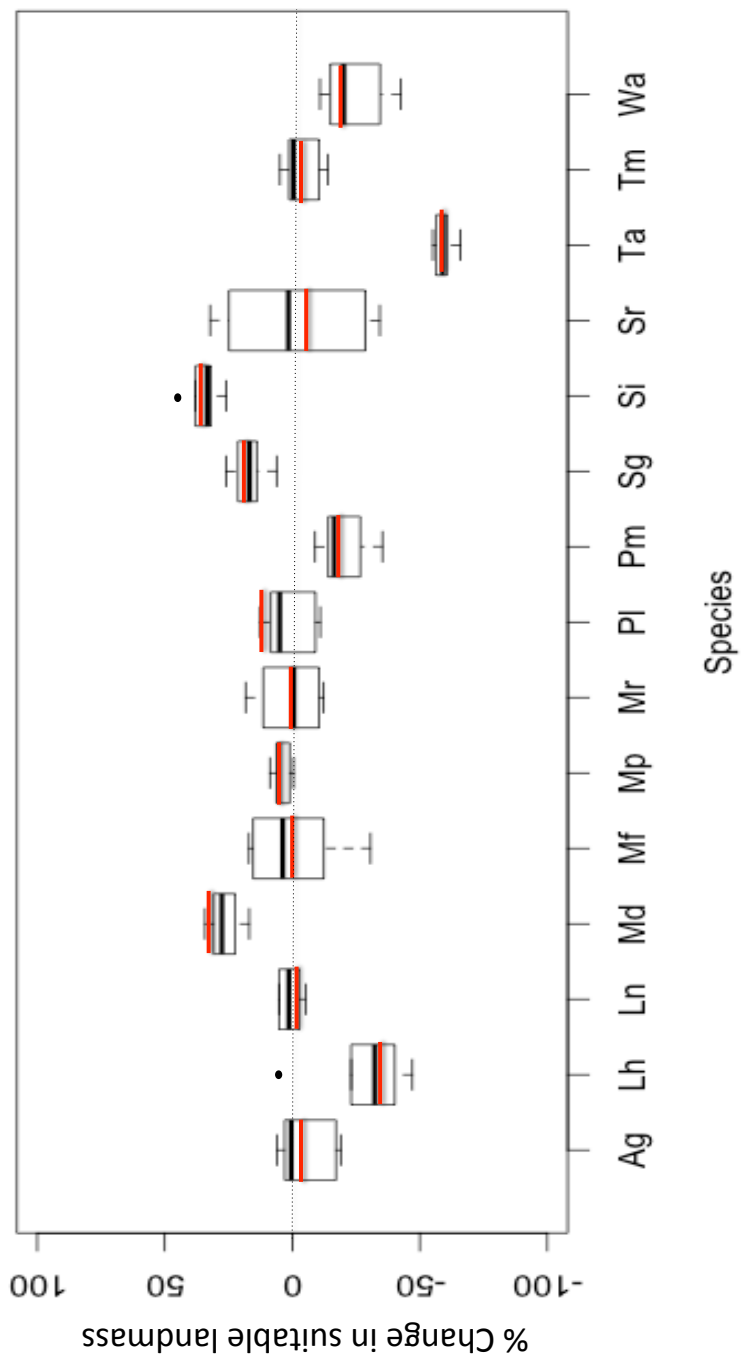
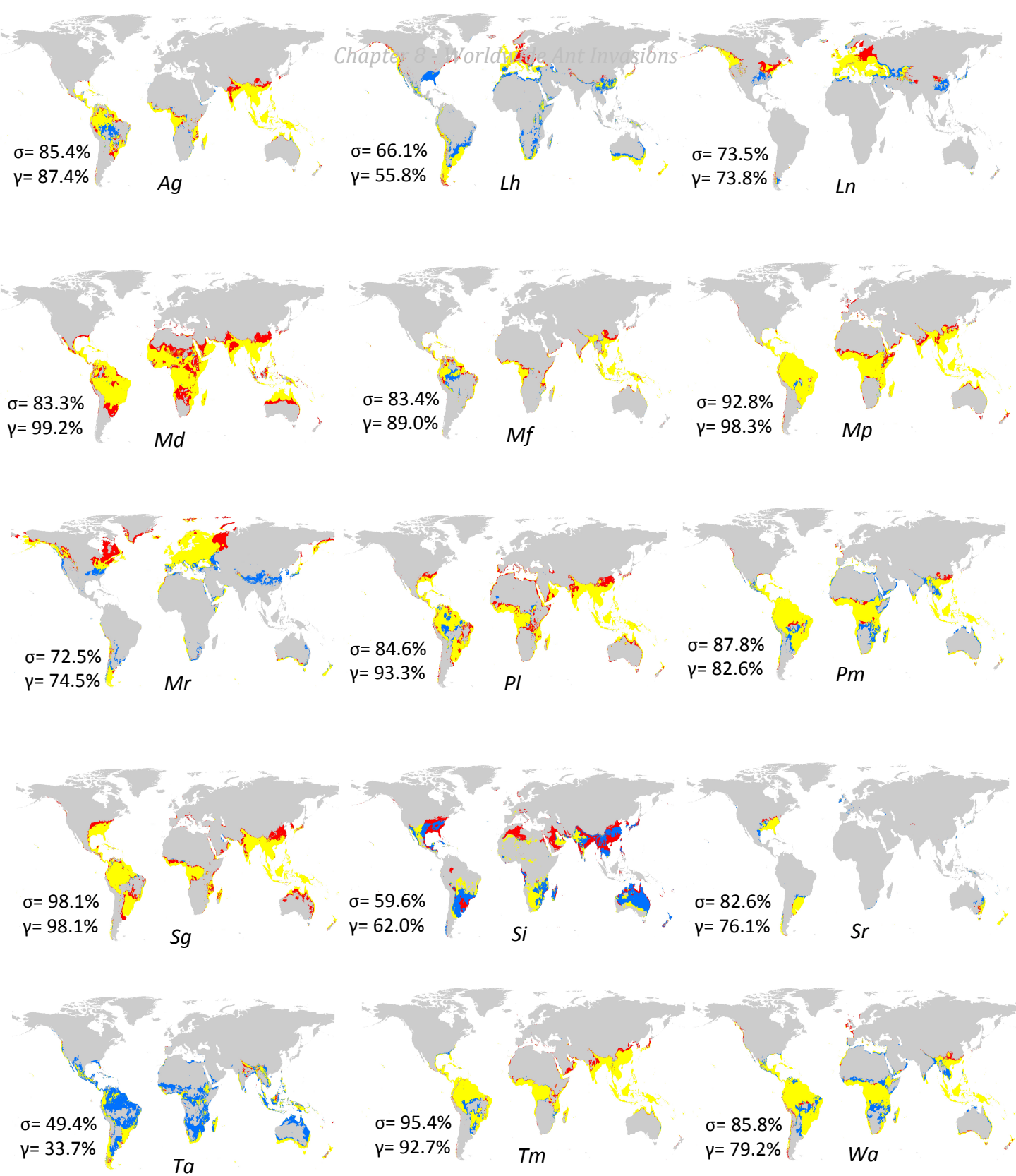


Fig. S3





# Future ant invasions in France

Cleo Bertelsmeier and Franck Courchamp



# Future ant invasions in France

CLEO BERTELSMEIER\* and FRANCK COURCHAMP

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**Ants are among the worst invasive species and can have tremendous negative impacts on native biodiversity, agriculture, estates, property and human health. Because invasive ants are extremely difficult to control, early detection is essential to prevent ant invasions, in particular through surveillance efforts at ports of entry. Here, we assess the potential distributions of 14 of the worst invasive ant species in France, under current and future climatic conditions. We generated consensus species distribution models, using five different modelling techniques, three Global Climate Models and two CO<sub>2</sub> emission scenarios. The projections show that France presented suitable areas for 10/14 species, including 4 that are among the “100 of the world’s worst invasive species”. Among these 10 species, 8 are predicted to increase their potential range with climate change. Areas with the highest concentration of potential invaders are mainly located along the coastline, especially in the South-West of France, but all departments appear climatically suitable for at least two invasive species. We provide a ranking of climatic suitability per species for 17 major airports and 14 maritime ports. Overall, the ports of entry with the highest suitability are located in Biarritz, Toulon and Nice and the species with the greatest potential distribution in France are *Lasius neglectus* and *Linepithema humile*, followed by *Solenopsis richteri*, *Pheidole megacephala* and *Wasmannia auropunctata*.**

Invasive ants | climate change | species distribution models | biological invasions | France

## INTRODUCTION

Biological invasions are among the most important drivers of species extinctions (Simberloff et al., 2013) and the number of introduced species has been increasing steeply over the last century due to human-mediated transport, such as tourism and commercial exchanges (Butchart & et al., 2010). One group of invasive species that is of particular concern for conservation are ants (Rabitsch, 2011; Holway et al., 2002). Because of their small size, they are easily transported by accident, in particular on fruits or on ornamental plants. Invasive ants have a tremendous impact on local biodiversity (Lach & Hooper-Bui, 2010), ecosystem functioning (Holway et al., 2002), economics (Harris & Barker, 2007) and even human and domestic animal health (Scanlan & Vanderwoude, 2006; Moreira et al., 2005). Once established, invasive ants become very difficult to eradicate (Hoffmann et al., 2010).

Ants can be best controlled during the first phases of the invasion when the population is still relatively small and confined to relatively small areas. Early detection is essential to prevent ant invasions, in particular through surveillance efforts at ports of entry (airports and maritime ports). The prioritization of surveillance should be based on assessments of the likelihood of establishment of different species. Although it is known that invasion risk depends on numerous biotic and abiotic factors, climate is thought to be the most important factor determining ant distributions at a global scale (Dunn et al., 2009; Sanders et al., 2007; Jenkins et al., 2011) and the invasion risks by ants (Roura-Pascual et al., 2011). As ants are ectotherms and particular sensitive to temperature and humidity, suitable climatic conditions are necessary for their establishment. Therefore, an evaluation of climatic suitability can serve as an important proxy for the invasion risk by ants. Previous studies have modelled the

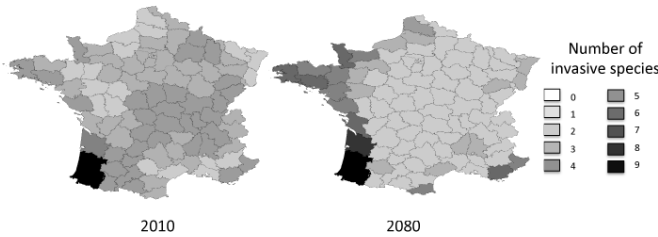
probability of establishment based on mechanistic (degree-day) models (Hartley & Lester, 2003; Hartley et al., 2010) and statistical species distribution models (Morrison et al., 2005; Roura-Pascual et al., 2004; Steiner et al., 2008; Bertelsmeier et al., 2013b, 2013a). Recently, it has been advocated to move beyond theoretical predictions and to implement practical management advice from species distribution models (Dawson et al., 2011). However, previous studies on potential distributions of invasive ants lack applicability for surveillance prioritization at a regional scale or at ports of entry for three reasons, (i) they make predictions at a global scale or (ii) they are concerned with theoretical questions about modelling methods and/or (iii) they are focused on single species. Therefore, there is a lack of relevant information to inform managers using species distribution models. This can only be achieved with a multi-species (global taxonomic) approach, which concentrates on a particular region and provides a ranking of relative suitability for different species for that region. Here, we provide such an assessment for 14 of the worst invasive ant species (IUCN SSC Invasive Species Specialist Group, 2012). We estimate climatic suitability for these species in France, which is a good model system for several reasons. First, France encompasses several climatic zones (coastal, continental, mountainous, Mediterranean) at a relatively small scale, thereby providing interesting regional differences in suitability. In addition, France is located in a temperate region and climate change is expected to affect the fitness of insects especially at these higher latitudes (Deutsch et al., 2008, but see Diamond et al. 2011), thereby potentially enabling tropical and subtropical species to invade. Such an assessment is very relevant for a country like France that uses a large part (51%) of its landmass for agriculture and plantations (Agreste, 2012) – which could be affected by invasive ants. Further, France occupies a central place for international trade and tourism (DGCIS, 2012). Bordered by three different seas and ocean and by five countries, it is ranked the first touristic destination in the world, with 81 million arrivals in 2012 (DGCIS, 2012) and the fifth country in volume of imported goods in 2010 and 2011 (WTO, 2011). In addition, France has many overseas departments and territories, including island territories in the Atlantic, Pacific and Indian oceans, as well as French Guiana on the South American coast. Many of these territories are tropical and subtropical and are currently invaded by several species of ants (IUCN SSC Invasive Species Specialist Group, 2012).

### Significance

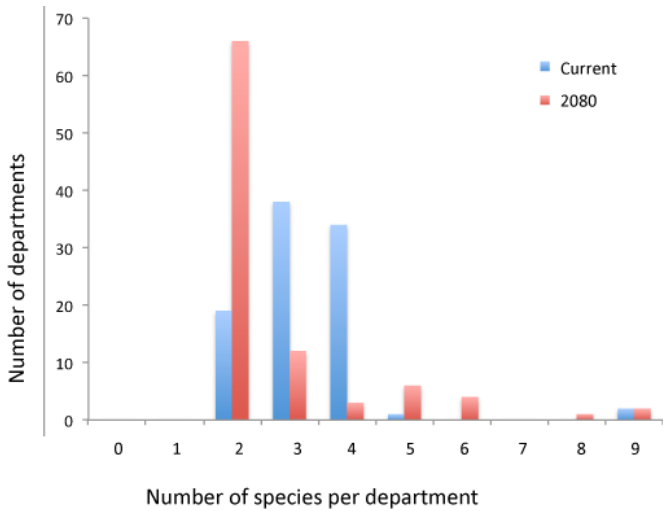
This paper is currently in press in *Environmental Conservation*



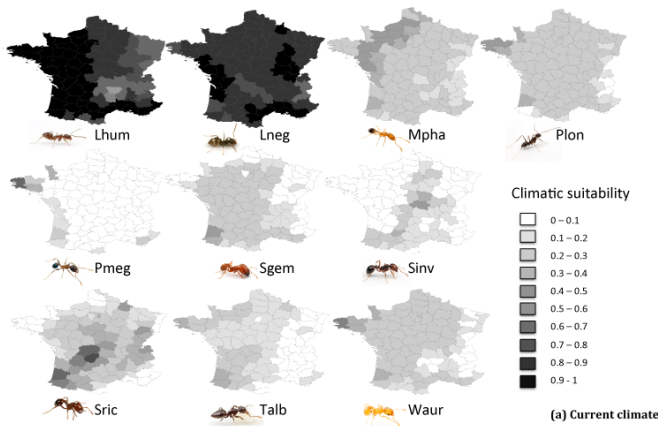
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**Fig. 1.** Number of potentially invasive ant species per department in France. The grey scale indicates between 0 and 9 potential invasive species.

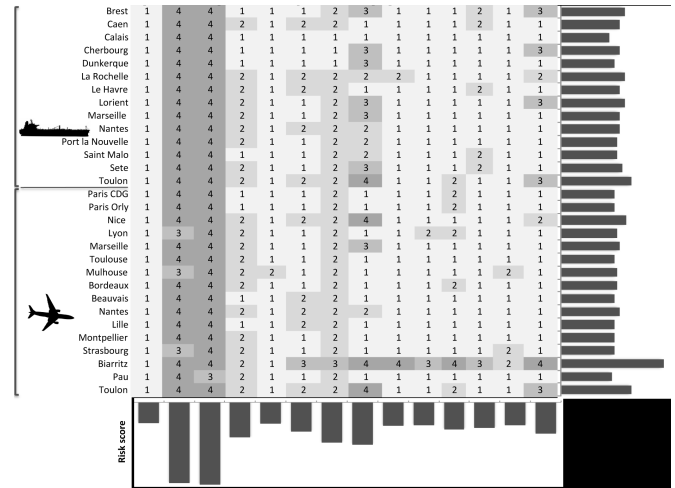


**Fig. 2.** Number of departments potentially invaded by 0 to 9 invasive ant species.

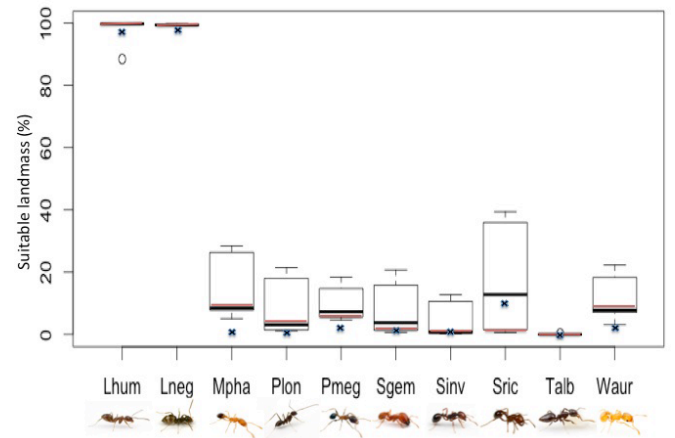


**Fig. 3.** a) Current mean climatic suitability within each of the 95 French metropolitan departments for 10 potential invasive species for whom France presents suitable climatic conditions (the other 4 species for which areas in France are entirely unsuitable are not included in this figure), b) changes in mean climatic suitability within each department by 2080. Ant pictures ©Alex Wild, used by permission.

These territories are characterised by disproportionate volumes of transportation of people and goods, which in addition benefit from facilitated imports under the regulation of the European Union. France also has privileged exchanges with many countries, some of which are former colonies. Consequently, there is an increased likelihood of accidental import of these species from tropical and subtropical regions.



**Fig. 4.** Climatic suitability scores for all major maritime ports and airports a) under current climatic conditions, b) with climate change (2080)



**Fig. 5.** Suitable landmass (%) under current climatic conditions (blue crosses) and the consensus model (red line). The box plot shows variation in prediction of future suitable landmass across the 6 climatic scenarios (mean ± s.d.). Ant pictures ©Alex Wild, used by permission.

Here, we use species distribution models to assess the amount of suitable landmass in France for 14 globally invasive ant species (Table 1). Of these species, five are on the Invasive Species Specialist Group's (ISSG) selection of "100 of the world's worst invasive alien species" (ISSG) (Table 1). To our knowledge, only two species (*L. humile* and *L. neglectus*) have colonized the mainland of France yet (i.e. live outside greenhouses or similar) (ISSG). The population of *L. humile* is part of the European supercolony that spans 6000 km from Portugal to Italy (Giraud et al., 2002). It has first been recorded in Southern France in 1906 (Blight et al., 2010) and its invasion is so far limited to the Mediterranean coastline. *L. neglectus* is a more recent invader, it has been described as a new species in 1990 (Cremer et al., 2008) and most records in France are past the year 2000 (Espadaler & Bernal, 2011). However, the species has reached a much larger distribution than *L. humile*. It has established along the Mediterranean coastline, but also in South-Western France, in the Alps (Annecy), Brittany (near Brest) and the centre of France (Paris, Tours) (Espadaler & Bernal, 2011). To our knowledge, no systematic eradication programs have been attempted.

The aim of this study is to map national and departmental suitability for 14 highly invasive ant species, both currently and with climate change. A department is an administrative division of France below the regional level and there are 96 departments on the French mainland. Using forecasts under current climatic conditions, we evaluate climatic suitability at a national, department and species-levels. In addition, we assess climatic suitability in the future, following 6 climatic scenarios (based on the combinations of 3 climatic models and 2 CO<sub>2</sub> emission scenarios), which have been pooled into a single consensus forecast for the year 2080. Finally, we provide a suitability ranking for the most important airports and maritime ports of France.

## METHODS

### 2.1. Species distribution data

Ecological niche models search for a non-random association between environmental predictors and species occurrence data to make spatial predictions of potential distribution. Because our models should include the full set of climatic conditions under which the target species can exist, we included occurrence points (presence-only data) from both invaded and native habitats (Beaumont et al. 2009). The data were sourced from the globally authoritative IUCN database for invasive species (IUCN SSC Invasive Species Specialist Group, 2012) as well as a database for ant distributions (Harris & Rees, 2004). We obtained additional points for *M. destructor* from Wetterer (2009). Data were excluded where the species were present in artificial climatic conditions, such as greenhouses, or when they were collected prior to the second half of the 20<sup>th</sup> century. In total, we used on average 237 points of occurrence per species to model the species' distribution. For models requiring absence data, 10,000 pseudo-absence (background) points were generated randomly.

This is a classic procedure because confirmed absence data is difficult to obtain for most species and requires great sampling efforts (Franklin, 2009). We have constrained the set of random points so that there are no points in the seas or the poles. It is however delicate to make too strong assumptions about 'unsuitable' habitat because the species are global invaders, present on several continents and have invaded a wide range of latitudes and habitats. It has been suggested that including background data from beyond the species' hypothesized potential distribution, or those that are environmentally dissimilar from the presence locations yield more plausible SDMs, especially if the purpose is to project species invasion or range changes under climate change (Franklin, 2009 and references therein).

### 2.2. Climatic predictors

We modelled the species niche based on 6 of the 19 bioclimatic variables provided by the WorldClim database (Hijmans et al., 2005), which were not collinear (pair-wise  $r_{\text{pearson}} < 0.75$ ) (Table S1) and contributed most to the Maxent model for each focal species. These bioclimatic variables are derived from monthly temperature and rainfall values from 1960-1990 (Hijmans et al., 2005) and are known to influence species distributions (Root et al., 2003). The distribution data comes from specimens that have been collected during the second half of the 20<sup>th</sup> century and coincide with the "current" climatic conditions.

Future climatic data were sourced from the 4<sup>th</sup> IPCC assessment report (GIEC, 2007). The projections were calibrated and statistically downscaled by the IPCC using the WorldClim data for 'current' conditions and therefore the projections can be compared. In order to consider a range of possible future climates, we used downscaled climate data from three climate models: the CCCMA-GCM2, the CSIRO-MK2 and the HCCPR-HADCM3 Global Circulation Models, (GIEC, 2007), which are among the most widely used climate models (Bradley et al., 2010; Sykes & Osborne, 2011). Similarly, we used the two extreme Special Report on CO<sub>2</sub> Emission Scenarios: the optimistic B2a and pessimistic A2a scenarios. We used a spatial resolution of 10 arcmin (approx. 18.5x18.5 km pixel). Predictions based on coarser resolutions are more likely to be controlled by climatic predictors, whereas fine-scale, patchy distributions at a smaller scale are more likely to be determined by micro-topographic variations or habitat fragmentation (Guisan & Thuiller, 2005). More details about the climatic predictors can be found in Bertelsmeier et al. (2013a, b).

### 2.3. Ecological Niche Modelling

Five machine learning modelling techniques were used to generate the consensual forecasts, two types of Support Vector Machines (1 class SVMs with parameters: kernel=Radial Base function,  $\gamma=1$ ,  $\sigma=0.05$ , 2 class SVMs with parameters: kernel= Radial Base function,  $\gamma=3$ , Cost=1), Artificial Neural Networks (parameters: type= Backpropagation ANN, Momentum=0.3, Learning rate=0.1) and Classification Trees (parameters: type= iterative, Number of trials=5, Window size=10, Pruning level=0.25) and finally the Maximum Entropy (Maxent) algorithm. Machine Learning methods are a set of algorithms that learn the mapping function or classification rule inductively from the input data (Elith et al., 2006). All models were run using the ModEco Platform with default parameters (Guo & Liu, 2010; Bertelsmeier et al., 2013a for additional details on model algorithms).

A clear limitation of modelling is that outputs are dependent on the specifically chosen input settings, in this instance the algorithms, global climate models and scenarios of human development. To minimise potential resulting variation, we conducted consensual forecasts (Araújo & New, 2007) of combined models using the five different modelling techniques above with each of six future climatic scenarios (based on three climate models and two CO<sub>2</sub> emission scenarios). The purpose of consensual forecasts is to separate the signal from the "noise" associated with the errors and uncertainties of individual models, by superposing the maps based on individual model outputs. Areas where these individual maps overlap are defined as areas of "consensual prediction" (Araújo & New, 2007). This is different from averaging the individual projections, as the area predicted by the consensual forecast can be smaller than any individual forecast if there is little spatial agreement (i.e., overlap) between individual forecasts.

The contribution of the individual models (i.e. the spatial prediction of "suitable range") was weighted according to their Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve in order to enhance contribution of models with higher model performance values (see below). Only binary projections (present or absent) have been combined to generate the consensus model because continuous outputs can have different meanings for different models and cannot be simply added together (Guo & Liu, 2010). The combination of the individual forecasts then yields a projection (the consensus model), where the value of pixels vary between 0 and 1 and can be interpreted as a probability of the species being present in each pixel (Araújo & New, 2007).

The consensus model was generated using all 30 individual projections, each based on a different combination of CO<sub>2</sub> scenario x climate models x modelling technique. Consequently, we obtained a single value per consensus model. We also calculated the standard deviation among climatic scenarios in order to show the extent of variation across forecasts.

### 2.4. Model validation

Model robustness was evaluated using the AUC of the ROC curve, which is a nonparametric threshold-independent measure of accuracy commonly used to evaluate species distribution models (e.g., Pearce & Ferrier, 2000; Roura-Pascual et al., 2009). We used the AUC because it does not depend on the selected classification threshold, and it readily indicates whether a model discriminates correctly between presence and absence points (Pearce & Ferrier 2000). AUC values range from 0 to 1, where a value of 0.5 can be interpreted as a random prediction. AUC between 0.5 and 0.7 are considered low (poor model performance), 0.7 – 0.9 moderate and >0.9 high (Franklin, 2009, and references therein). For model evaluation, the data needs to be split into a training and a test group. Here, we used 10-fold cross-validation, whereby the data has been split into 10 equal parts, with 9/10 of the observations used to build the models and the remaining 1/10 used to estimate performance; this was repeated ten times and the estimated performance measures were averaged (Franklin, 2009; Fielding & Bell, 1997). More details about the ecological niche modelling and model validation can be found in Bertelsmeier et al. (2013a, b).

### 2.5. Assessing climatically suitable areas

Studies with *a priori* objectives, may use a range of different threshold values (Nenzén & Araújo, 2011). As this was not our case here, we applied a limit whereby all pixels with a probability of presence exceeding 0.5 were classified as "suitable" areas, as is frequently done for binary classification for species distribution modelling (Franklin 2009; Klamt et al. 2011). Spatial analyses were carried out using DIVA-GIS (Hijmans et al., 2001) and Arcgis v.9.3.

We analysed which departments had the highest number of potential invaders, based on a simple presence/absence score. If at least 1 pixel within a department was suitable, the species was counted as a potential invader in that department.

At the species-level, we provide maps of the current potential distribution of all species for which at least 1 pixel exceeded the classification threshold of 0.5. We calculated the mean suitability per department for all of these species. Mapping relative differences between suitability levels goes beyond the use of binary classification and provides more information on the relative climatic suitability of departments that have been classified as "suitable". The use of this "quality" assessment has been advocated recently, especially in the case of conservation assessments and invasive species (Bertelsmeier et al., 2013a).

### 2.6. Recommendations at ports of entry

We included in this study all 17 airports in France with more than 500,000 passengers in 2012 (Union des aéroports français, 2012) and 14 major maritime ports on France (Benmessaoud, 2013). We scored the relative invasion likelihood for each species and port of entry based on climatic suitability: "Very low" suitability (0-0.25) was assigned the score 1, "low" suitability (0.25-0.5) was 2, "high" suitability (0.5-0.75) was 3 and finally "very high" suitability" (0.75-1) was 4. We then calculated the total climatic suitability score for each port of entry (by summing the climatic suitability scores of all species of the port of entry) and for each species (by summing the species' scores of all ports of entry).

### 3. RESULTS

All AUC values were between 0.787 and 0.998 (mean 0.921, s.d. 0.053), indicating an overall good to excellent ability to predict the species' presence based on the consensus models.

#### 3.1. Current potential distribution

Under current climatic conditions, almost the entire landmass in mainland France presented suitable climatic conditions for 10 out of 14 invasive ant species. The highest proportion of landmass was suitable for *L. neglectus* and *L. humile*, followed by *S. richteri*, *P. megacephala* and *W. auropunctata* (Table 1). For four major global invaders included in this analysis, *A. gracilipes*, *M. destructor*, *M. floricola* and *T. melanocephalum*, France did not present suitable climatic conditions.

All of the French mainland departments had at least two potential invaders (*L. neglectus* and *L. humile*), but most were suitable for three (38 departments) or four (34 departments) invasive ants (Fig. 1a). For example, Ile-de-France presents suitable climatic conditions for 3 invasive species. At the extreme, the departments Pyrénées-Atlantiques and Landes in the South-West could each be invaded by nine ant species (Fig 2).

At the species-level, there were important regional differences concerning the location of the most suitable climatic conditions. Overall, the absence of an expected North-South division was striking for most species. Rather, most species showed an East-West gradient of climatic suitability, the most suitable departments being located on the West coast (Fig. 3a). An exception to this pattern is *L. neglectus*, which had highly suitable conditions across the whole of France. Several species found highly suitable conditions in Brittany or Normandy (*M. pharaonis*, *T. albipes*, *P. longicornis*, *P. megacephala*, *W. auropunctata*). As opposed to most other species, two species (*S. invicta* and *S. richteri*) did not have suitable conditions near coastal regions but rather inland.

The ports of entry with the highest suitability score were Biarritz airport (42, out of a total of 56), followed by Toulon Hyères airport (29), Toulon maritime port (29), Nice airport (27) and the maritime ports of Brest, La Rochelle and Lorient (26 each)(Fig. 4a). Species with the overall highest suitability score at ports of entry in France were *L. neglectus* (119, out of a total of 120) and *L. humile* (117), followed by *P. megacephala* (61) and *P. longicornis* (58).

#### 3.2. Impacts of climate change on ant invasions

The four species that had no climatically suitable areas in France under current climatic conditions (*A. gracilipes*, *M. destructor*, *M. floricola*, *T. melanocephalum*) did not have any suitable areas in France under climate change either. Among the ten species, which could potentially invade France, the potential distribution in France increased for eight (Fig. 5). The highest increase was found in *M. pharaonis*, followed by *W. auropunctata*, *P. megacephala* and *P. longicornis* (Table 1). The potential distribution decreased only for *S. richteri* and *T. albipes* (Table 1).

The places with the highest concentration of potential ant invaders shifted in space with climate change (Fig. 1b). By 2080, the whole western coastline of France had a higher number of invasive ant species than inland areas. With climate change, the number of departments suitable for only 2 invasive species increased, totalling 66. In parallel, there was also an increase in the number of departments suitable for more than 4 species, reaching 13 (Fig. 2).

With climate change, the suitability scores of many departments (Fig. 3b) and ports of entry (Fig 4b) increased, especially along the western coastline. The highest increases in relative suitability were found in *L. humile* (mostly in the Eastern part which was slightly less favourable under current conditions), *M. pharaonis*, *P. megacephala* and *W. auropunctata* (highest increase in Brittany) (Fig. 3b). The highest suitability score was still found in Biarritz airport (41), followed by several ports that now had suitability scores exceeding 30: Brest port (33), Lorient port (32),

Toulon port, Nice airport, Bordeaux Mérignac airport and Toulon airport (31 each). The highest relative increases in suitability scores per species were found in *M. pharaonis* (+29), *S. geminata* (+21) and *W. auropunctata* (+20).

### DISCUSSION

Our consensus models predicted that France had suitable climatic conditions for 10 out of 14 of the worst invasive ant species, including 4 that are on the « 100 of the world's worst invasive alien species » list of the IUCN (Lowe et al., 2000). Areas with the highest concentration of potential invaders are mainly located along the coastline, especially in the South-West of France, but all departments appear climatically suitable for at least two species. Among potential ports of entry, the airport of Biarritz is by far the most at-risk and almost all species should be closely monitored for there. Several species were at high-risk of interception in many ports of entry, including the Argentine ant and the garden ants, which both scored the highest possible climatic suitability on our scale. With climate change, the potential distribution was predicted to increase for 8 out of 10 species in France. The most suitable area by 2080 extended along the western coastline, from the Pyrenees to Northern France. However, inland departments were predicted to receive a lower number of invasive species than under current climatic conditions.

Our models had good to excellent performance (AUC) but nevertheless they share a certain number of underlying assumptions common to all species distribution models (Guisan & Thuiller, 2005; Sinclair et al., 2010). For example, they require niche conservation, i.e. the species requirements have to remain the same in space and time. Although it is known that this is not always the case for invasive species, niche shifts remain relatively rare (Petitpierre et al., 2012). Furthermore, these models do not take into account biotic interactions or microclimatic conditions, which may determine at a very local scale whether or not a particular invasive species ultimately becomes established in a given area. In addition, the model outputs only show the climatically suitable areas but the actual distribution and spread of the invasive ants depends mostly on human-mediated transport as most of the species form new colonies by budding (Holway et al., 2002). This strongly limits the initial colonization to areas adjacent to points of introduction (Holway et al. 2002). An important exception is *S. invicta*, which occurs both as a monogyne and a polygyne form and winged queens of the monogyne colonies are capable of travelling several kilometres away from their natal nest (Tschinkel 2006). But for most invasive ants, the distance to human infrastructures is an important factor determining actual invasion risk. The association of invasive ants with urban ecosystems is especially relevant at a local scale (Roura-Pascual et al. 2011). Nevertheless, species distribution models can reveal general patterns and deliver useful approximations, which are important for ranking species according to their potential to invade a given area (Warren, 2012; Araujo & Peterson, 2012). Any particular modelling algorithm has its set of assumptions. This is why we do not base our conclusions on the results of a single modelling method, however widespread its use may be, but combine a range of different forecasts in a single consensus model (Araújo & New 2007). Climatic suitability, which we have assessed here, is a necessary precondition for successful establishment of an invasive species, even though it may eventually be hindered by other biotic or abiotic factors. The comparison of relative suitability (or « quality ») of areas in different departments for different species can serve as an indicator of which species need to be most monitored, and where (Bertelsmeier et al., 2013a). For example, relative climatic suitability has probably played a role in the recent displacement of Argentine ants by a newly invasive ant species from areas that the Argentine ant had invaded and dominated for several years. This presumably arose because these areas

were situated in the range margins of the climatic niche of the Argentine ant and relative climatic suitability was higher for the other species, *Pachycondyla chinensis* (Rice & Silverman, 2013). Information on relative suitability of different species, such as the assessment that we provide here, can serve as a basis for the prioritization of management efforts.

Once invasive ants become established in a climatically suitable area, it is notoriously difficult to control or eradicate them. A range of commercialized products exists, but no universal bait exists because of differences in dietary preferences among species (Hoffmann et al., 2010). These products differ in their environmental acceptability, but always have negative impacts on native taxa to some extent. In some cases, these measures can be complemented by habitat modification such as fire (Hoffmann & O'Connor, 2004), or drainage restriction (Holway & Suarez, 2006), but these modifications can negatively impact the ecosystem on their own by creating disturbance. The greater the extent of an invasion, the higher the environmental impacts of management attempts and the difficulty of achieving successful eradication, provided this is still feasible (Simberloff, 2003). In general, reactive programs have proved far more expensive than proactive programs (Kaiser & Burnett, 2010). However, species-specific protocols are needed before taking action (Hoffmann et al., 2010). Ill-conceived treatments can even have the adverse effect, for example the invasion of *S. invicta* in the Southern United States seems to have actually increased following chemical treatment (Tschinkel, 2006).

Yet, historically, ant management has been reactive, only starting after the detection of an incursion, even though for ants as well a pro-active approach has been advocated (Hoffmann et al., 2010). The first step of such an approach is to carry out risk analyses of the target species that may become established, or even better, of any species that may become established within a target region. Our study can serve as a basis for a pro-active ant management plan in France, based on privileged surveillance of certain species according to the department and the port of entry. These steps require increased detection protocols at ports of entry, which is now standard within New Zealand since the detection of *S. invicta* at Auckland International Airport in 2001 (Hoffmann et al., 2010). The numerous intercepted ant species in the US demonstrate that the likelihood of introducing ants inadvertently is high if no surveillance measures are taken

(Suarez et al., 2005). In countries with well-developed monitoring programs for invasive species, government departments responsible for food-production industries or environmental issues have the expertise to conduct invasive ant control programs in addition to some non-governmental entities such as local land management organizations (Hoffmann 2010). Developing invasive species monitoring programs would be especially important for a country like France which has a great amount of commercial and touristic exchanges (DGCIS, 2012; WTO, 2011). Further, immediate treatment options have to be planned for the species most at risk of becoming invasive, in order to act quickly as soon as an incursion is detected. Immediate action increases the chances of successful eradication enormously (Simberloff, 2003), lowering its cost and reducing the extent of collateral impact on native fauna. Public education can be important for increasing acceptance of management actions and encouraging the public to signal early detection of the target species (Hoffmann et al., 2010). A useful first step would be to develop identification tools for at-risk species (species determination keys and profiles) that may be distributed at ports of entries or to increase surveillance efficiency by raising public awareness. Lastly, actions may require permits and registrations for poison use and it is recommended to remove these obstacles prior to incursions in order to eliminate delays in the management actions (Hoffmann et al., 2010).

The regional approach used here can serve as a good basis to forecast the potential distribution of known global invaders, listed by the IUCN. However, future research should aim at developing predictive tools to identify additional potential invasive species in order to achieve a more exhaustive assessment for a taxonomic group. For example, this might be based on traits associated with invasiveness, which could be combined with an assessment of geographic likelihood of establishment – such as provided here.

Our models identify several potential invasive ant species in France and highlight regions with a high risk of multiple invasions. We strongly recommend using this spatialized ranking of species and areas to prioritize surveillance efforts and pro-active management options.

#### Acknowledgements .

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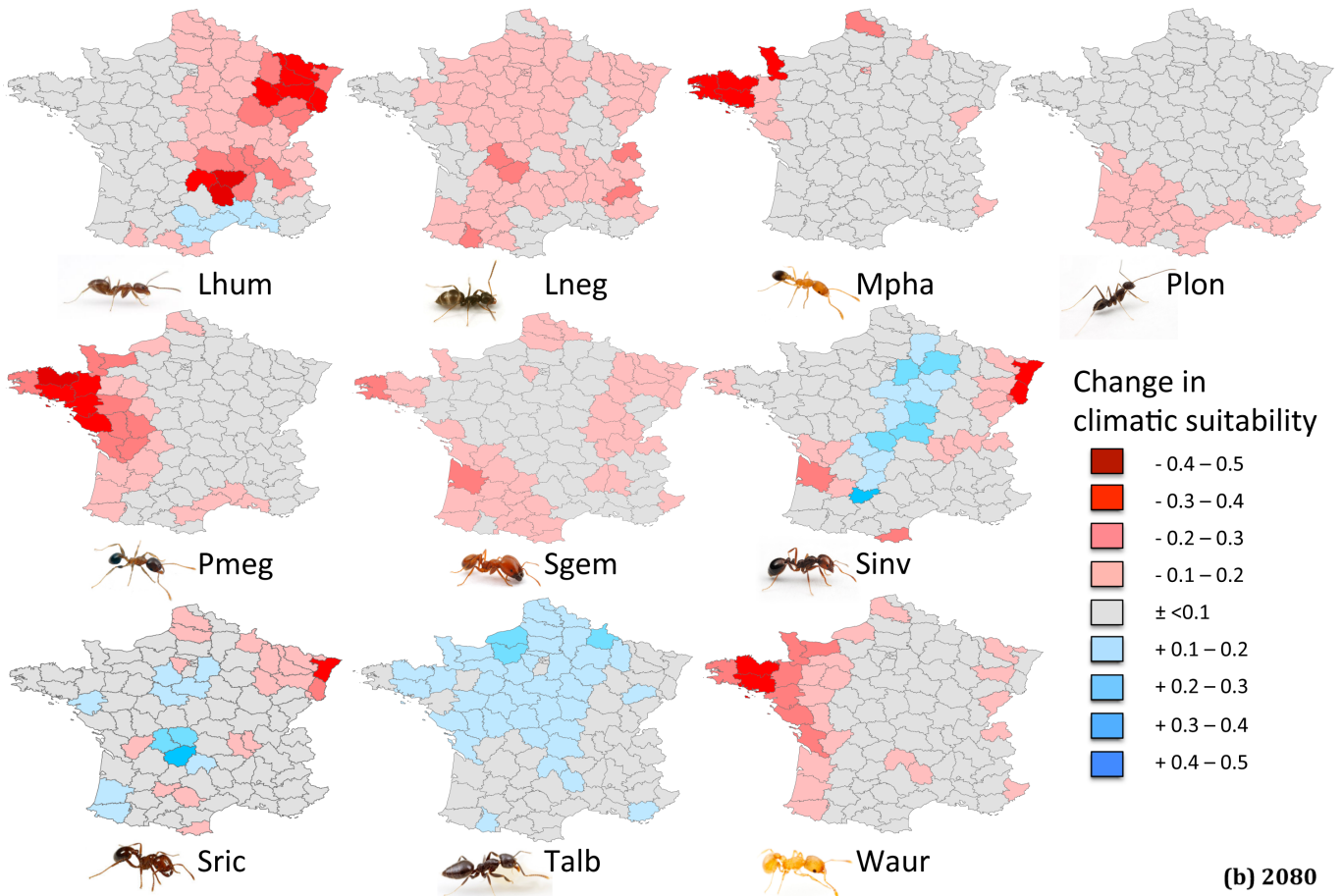


Fig. 3: b) changes in mean climatic suitability within each department by 2080.

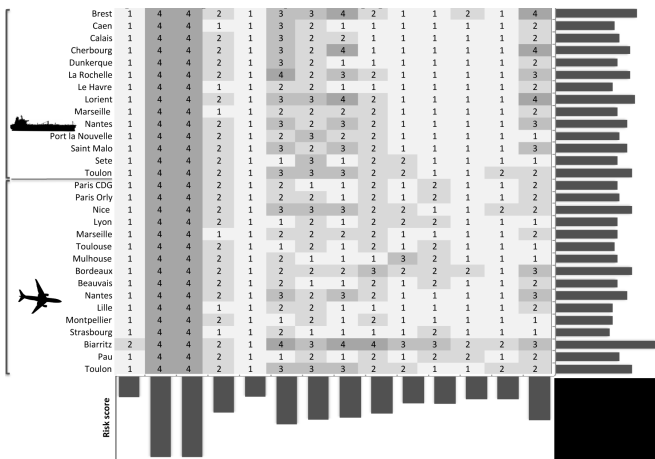


Fig. 4: b) Climatic suitability scores for all major maritime ports and airports with climate change (2080)















Image	Scientific name	Common name	Region of origin	Exotic elsewhere	Distribution points used for modelling	Suitable landmass in France currently (km <sup>2</sup> )	Suitable landmass in France currently (%)	Change in suitable landmass by 2080 (km <sup>2</sup> )	Change in suitable landmass by 2080 (%)	100 of the worst invasive species (IUCN)	Principal impacts			Key references
											Impact on biodiversity	Disruption of ecosystem processes	Economic impact	
	<i>Anoplolepis gracilipes</i>	Yellow crazy ant	Asia or Africa	Africa, Asia, South America, Australia, Oceanic islands	369	0	0	0	0	✓	✓	✓	✓	O'Dowd et al. (2003), Abbott (2005), Abbott & Green (2007), Hill et al. (2003), Harris (2005)
	<i>Linepithema humile</i>	Argentine ant	South America	All continents except Antarctica, many islands	519	652,378	96.6	22,159	3.4	✓	✓	✓	✓	Tsutsui et al. (2000), Holway (1999), Suarez & Bolger (1998), Human & Gordon (1996), Giraud et al. (2002)
	<i>Lasius neglectus</i>	Invasive garden ant	Asia Minor	Europe, Iran, Kyrgyzstan, Uzbekistan	153	663,751	98.3	9,025	1.4	✓	✓	✓	✓	Cremer (2008), Ugelvig (2008), Espadaler (2001), Espadaler (2007), Harris (2005)
	<i>Monomorium destructor</i>	Destroyer ant	India	Australasia-Pacific, North America, South America	116	0	0	0	0	✓	✓	✓	✓	Wetterer (2009), Harris & Barker (2007), Harris (2005)
	<i>Monomorium florcola</i>	Flower ant	Asia	All continents except Antarctica, many islands	228	0	0	0	0	✓	✓	✓	✓	Wetterer (2010), Harris (2005)
	<i>Monomorium pharaonis</i>	Pharaoh ant	Africa	All continents except Antarctica	112	1,749	0.3	71,569	4090	✓	✓	✓	✓	Moreira (2005), Wetterer (2010), Harris & Barker (2007)
	<i>Paratrechina longicornis</i>	Crazy ant	Asia or Africa	All continents except Antarctica	476	2,333	0.3	24,648	1056	✓	✓	✓	✓	Harris (2007), Harris (2005)
	<i>Pheidole megacephala</i>	Big-headed ant	Africa	All continents except Antarctica	208	28,579	4.2	27,436	96	✓	✓	✓	✓	Hoffmann et al. (1999), Vanderwoude et al. (2000), Hoffmann & Parr (2008), Wetterer (2007)
	<i>Solenopsis geminata</i>	Tropical fire ant	Central America	All continents except Antarctica	443	7,582	1.1	15,293	201.7	✓	✓	✓	✓	Harris (2005)
	<i>Solenopsis invicta</i>	Red imported fire ant	South America	Australia, North America, Pacific islands, Caribbean islands	88	3,791	0.6	21	0.6	✓	✓	✓	✓	Ross et al. (1996), Morrison et al. (2004), Gorelli & Annett (2000), Morrison (2002)
	<i>Solenopsis rudereri</i>	Black imported fire ant	South America	North America	66	62,992	9.3	-53,02	-84	✓	✓	✓	✓	Harris (2005)
	<i>Technomyrmex aliphus</i>	White-footed ant	Indo-Pacific	Asia, Australia, Africa	60	1,458	0.2	1458	-100	✓	✓	✓	✓	Harris (2005)
	<i>Tapinoma melanocephalum</i>	Ghost ant	Asia or Africa	Australasia-Pacific, Europe, North America, South America	335	0	0	0	0	✓	✓	✓	✓	Moreira (2005), Harris & Barker (2007), Harris (2005)
	<i>Wasmannia auropunctata</i>	Electric ant	South America	Africa, North America, South America, many islands	261	14,581	2.1	52,578	360.6	✓	✓	✓	✓	Harris & Barker (2007), Clark et al. (1982), Harris (2005)

Table 1

	Ag	Lh	Ln	Md	Mf	Mp	Pl	Pm	Sg	Si	Sr	Ta	Tm	Wa
Annual mean temperature			x		x	x			x		x		x	
Mean diurnal range	x		x	x	x	x	x		x		x	x	x	
Isothermality	x		x		x		x		x	x	x	x		
Temperature seasonality			x											x
Maximum temperature of warmest month		x				x	x	x				x		
Minimum temperature of coldest month				x			x							
Temperature annual range		x		x	x	x		x					x	x
Mean temperature of wettest quarter					x					x			x	
Mean temperature of driest quarter		x									x			
Mean temperature of warmest quarter														
Mean temperature of coldest quarter	x	x						x		x		x		x
Annual precipitation														
Precipitation of wettest month	x	x							x					
Precipitation of driest month										x	x		x	x
Precipitation seasonality				x				x						x
Precipitation of wettest quarter								x						
Precipitation of driest quarter									x					
Precipitation of warmest quarter	x		x	x	x	x	x		x	x	x	x	x	
Precipitation of coldest quarter	x	x	x	x		x	x	x		x		x		x

Table S1 The 6 most relevant climatic variables for predicting each species' presence. The selected variables are not collinear (Pearson  $r < 0.75$ ) and have the highest contribution to the Maxent model. Ant species codes: Ag= *A. gracilipes*, Lh= *L. humile*, Ln= *L. neglectus*, Md= *M. destructor*, Mf= *M. floricola*, Mp= *M. pharaonis*, Mr= *M. rubra*, Pl= *P. longicornis*, Pm= *P. megacephala*, Sg= *S. geminata*, Si= *S. invicta*, Sr= *S. richteri*, Ta= *T. albipes*, Tm= *T. melanocephalum*, Wa= *W. auropunctata*.





# The impact of climate change changes over time

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## The impact of climate change changes over time



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## ABSTRACT

Species distribution models (SDMs) have become an important tool to predict the impact of climate change on the distribution of a given species. Generally, projections for a chosen time horizon in the future are compared with the size of the species' current distribution. In this study, we show that selection of the target time horizon can qualitatively alter the prediction of a species' future distribution. We illustrate this by assessing the potential distribution of 15 invasive ant species in 2020, 2050 and 2080 at a global scale. Our results indicate that for 6 out of the 15 species modelled, the trend of potential habitat size (i.e., decrease or increase) changed over time following climate change. In four species, the sign of the trend changed, from an initial expansion to a subsequent reduction or vice versa, depending on the date projected to. In some cases, these changes were great (e.g., from an initial increase of 36.5% in 2050 to a decrease of –64.3% in 2080). Our findings stress the importance of using several projection horizons to avoid misled species management decisions.

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## 1. Introduction

Many species from diverse taxonomic groups have already been affected by anthropogenic climate change, forcing them to change their phenology, physiology or distribution (Bellard et al., 2012). But climate change is happening at such a fast rate that many species will not be able to adapt rapidly enough. In fact, a large proportion of global biodiversity is predicted to go extinct before the end of this century (Bellard et al., 2012; Pereira et al., 2010). One way for species to persist, despite climate change, is to change/shift their geographic distribution. Shifts in species distributions will be one of the most dramatic consequences of climate change. Understanding the potential impacts of climate change on species' distributions is therefore crucial to enable stakeholders and biodiversity managers to make informed decisions to mitigate biodiversity loss (Pressey et al., 2007). Currently, the tool most widely used to predict species' future distributions are species distribution models (Sinclair et al., 2010; Pereira et al., 2010). This approach is based on the assumption that a species' current habitat reflects its ideal climatic conditions and is in equilibrium with its climatic niche. Species distribution models relate the species' current distribution to a set of climatic variables, which define its "climatic niche". It is then possible to project the species' niche to future climatic scenarios, based on different combinations of CO<sub>2</sub> emission scenarios and global circulation models. Projections at different dates in the

future can then be compared to the current climatically suitable area to evaluate changes in a species' potential distribution. A recent review has shown that almost all major global studies on the impact of climate change on biodiversity project to a single future time horizon, which can vary widely among studies, and is usually between 2050 and 2100 (Bellard et al., 2012). The choice of that time is rarely discussed and management recommendations are made based on a single "snapshot" in time. This implicitly assumes that the trend of the impact of climate change on a species' distribution will be the same in, for example, 2050 as in 2100. For example, if the potential range of a species decreases with climate change, it should decrease further at a later date. Conversely, a species that benefits from climate change is supposed to do so at different time horizons in the future. Quantitative differences are to be expected as climate change is continuing. The intuitive expectation is that climate change will accentuate any change in a species' distribution observed at an earlier date. Whether linear or non-linear, there is an implicit assumption that potential species' ranges, which expand by 2050, should further expand at a later date and that potential ranges which start by retracting should retract further.

In this study, our aim was to test the hypothesis that the choice of the future time horizon does not qualitatively influence the prediction of the trend of climatically suitable habitat for a given species. We used climatic data, which was available for three future time periods, which are in fact averages over 10-year periods and are centred around three dates in the future (2020, 2050, 2080) (Hijmans et al., 2005). For clarity, we will refer to those three dates in this paper. Using a range of 3 different time horizons for our projections allowed us to

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challenge the implicit assumption that the effects of climate change on species distributions are generally unidirectional and monotonic.

As a model system, we used 15 species of the same family and comparable ecology, in order to draw robust conclusions. We chose ants because they are widespread and dominant members of many ecosystems. Because they are poikilotherms, many features of their biology are very sensitive to temperature and humidity, including foraging (Brightwell et al., 2010), oviposition rate (Abril et al., 2008), and survival (Abril et al., 2010). It has been shown that climate is the most important factor in determining their distribution (Roura-Pascual et al., 2011) and therefore, climate change is highly relevant to predict future invasions of ants (Bertelsmeier et al., 2013). We also focused on invasive ants, because they allowed us to assess distributions at a global scale. Additionally, their projected distributions are of paramount importance for conservation biology. These 15 invasive ant species are responsible for numerous species displacements and local extinctions, as well as the perturbation of many interspecific relationships and ecosystem functions (Holway et al., 2002; Rabitsch, 2011; Lach and Hooper-Bui, 2010). In addition, many of these species are important agricultural pests (Rabitsch, 2011) and a nuisance to humans because they have a powerful sting and may transmit pathogens (Moreira et al., 2005). Management measures against these invasive ant species primarily rely on predictions of their current and future invasion “risk zones” (Hoffmann et al., 2010). In our study, we assessed the temporal change in potential habitat of 15 invasive ant species out of 19 listed by the Invasive Species Specialist Group of the IUCN (Lowe et al., 2000). All of these 15 species are known for their impacts on native species or human health and are present on several continents (IUCN SSC Invasive Species Specialist Group, 2012).

The 15 species are the Argentine ant, *Linepithema humile*, the yellow crazy ant, *Anoplolepis gracilipes*, the invasive garden ant, *Lasius neglectus*, the destroyer ant, *Monomorium destructor*, the flower ant, *Monomorium floricola*, the pharaoh ant, *Monomorium pharaonis*, the European fire ant, *Myrmica rubra*, the long-horned ant, *Paratrechina longicornis*, the big-headed ant, *Pheidole megacephala*, the tropical fire ant, *Solenopsis geminata*, the red imported fire ant, *Solenopsis invicta*, the black imported fire ant, *Solenopsis richteri*, the white-footed ant, *Technomyrmex albipes*, the ghost ant, *Tapinoma melanocephalum* and the electric ant, *Wasmannia auropunctata*.

We assessed the amount of climatically suitable landmass for each of these 15 species, with species distribution models at four different time horizons (current, 2020, 2050, 2080). The quantification of the effect of climate change on predicted suitable area worldwide at three future points in time allowed us to examine, for each species, the trend of these effects, and their possible reversal.

## 2. Materials and methods

### 2.1. Species distribution data

Species distribution models search for a non-random association between environmental predictors and species occurrence data to make spatial predictions of its potential habitat (Franklin, 2009). Because our models should include the full set of climatic conditions under which the species can thrive, we included occurrence points from both its invaded and native habitats (following Liu et al., 2011; Rödder and Lötters, 2009; Beaumont et al., 2009; Broennimann et al., 2007). It has been shown that models calibrated based on only native range data often misrepresent the potential invasive distribution and that these errors propagate when

estimating climate change impacts (Beaumont et al., 2009; Broennimann et al., 2007).

In total, we used an average of 239 points of occurrence per species to model the species' distribution (366 points of occurrence for *A. gracilipes*, 153 for *L. neglectus*, 519 for *L. humile*, 116 for *M. destructor*, 228 for *M. floricola*, 112 for *M. pharaonis*, 123 for *M. rubra*, 476 for *P. longicornis*, 208 for *P. megacephala*, 443 for *S. geminata*, 88 for *S. invicta*, 66 for *S. richteri*, 59 for *T. albipes*, 335 for *T. melanocephalum* and 288 for *W. auropunctata*) (Fig. A1 Supplementary Online Material). The number of points was sufficient to achieve good model performance for all species (Table A1 in Supplementary Online Material). The occurrence records came from the literature, researchers, government agencies, student projects and private collectors, compiled in two public databases; the ISSG database for invasive species (IUCN SSC Invasive Species Specialist Group, 2012) a database for ant distributions (Harris and Rees, 2004). We did not include points where the species was present in artificial climatic conditions, such as greenhouses. For this, points were removed from the distribution whenever they were obviously lying outside the species requirements. For models requiring absence data, 10 000 randomly and globally distributed pseudo-absence (background) points were generated.

### 2.2. Climatic predictors

We modelled the species niche based on 6 of the 19 bioclimatic variables provided by the Worldclim database (Hijmans et al., 2005). We selected for each species the 6 variables, which had the highest contribution to the Maxent model (most relevant for determining its distribution) and that were not collinear (pair-wise  $r_{\text{Pearson}} < 0.75$ ) (Table A2). The bioclimatic variables are derived from monthly temperature and rainfall values from 1960 to 1990 (Hijmans et al., 2005) and are known to influence species distributions (Root et al., 2003). We used a spatial resolution of 10 arcmin (approx.  $18.5 \times 18.5$  km pixel).

Future climatic data was also provided by the Worldclim database which uses data from the 4th IPCC assessment report and which had been calibrated and statistically downscaled to match the data for “current” conditions (GIEC, 2007). In order to consider a range of possible future climate conditions, we modelled the species potential future distribution based on downscaled climate data from the 3 available Global Circulation Models (GCMs) provided by different climate modelling centres: The CCCMA-GCM2 model, the CSIRO-MK2 model and the HCCPR-HADCM3 model (GIEC, 2007). These GCMs are frequently used in species distribution modelling (Bradley et al., 2010; Synes and Osborne, 2011). In addition, projections for two different Special Report on CO<sub>2</sub> Emission Scenarios (SRES) were included in our models: the optimistic B2 scenario (CO<sub>2</sub> concentration 800 ppm, 1.4–3.8 °C temperature increase) and the pessimistic A2 scenario (CO<sub>2</sub> concentration 1250 ppm, 2–5.4 °C temperature increase) (GIEC, 2007). In total, we used 6 future climatic scenarios per future time horizon (2 SRES  $\times$  3 GCMs).

### 2.3. Species distribution modelling

We used five different machine learning modelling techniques, which are among the most widely used algorithms and are known for their robustness (Franklin, 2009) to generate the ensemble forecasts. Machine learning methods are among the recently developed tools especially designed for modelling complex relationships and prediction (Lorena et al., 2011) and their predictive performance often exceeds that of more conventional techniques (Elith and Leathwick, 2009; Guyon and Elisseeff, 2003). They are used to characterise the function that explains species distribution based on climatic variables inductively, directly from the input

data (Franklin, 2009). That means that these types of learning algorithms do not assume a certain type of distribution. Their predictive performance often exceeds that of more conventional techniques (Elith and Leathwick, 2009).

The first two models are based on Support Vector Machines (SVM), which are a new generation of learning algorithms. In a classification problem, two-class SVMs seek to find a hyperplane that maximally separates the two target classes. Recently, one-class SVMs have also been developed. They distinguish one specific category from all other categories. We included a one-class SVM in addition to the two-class SVM because it is a promising new approach in species distribution modelling (Guo et al., 2005).

Third, we used Artificial Neural Networks (ANNs) that have been commonly used to model complex relationships (Manel et al., 1999). In particular, ANNs have been successfully used to predict species distributions (Franklin, 2009; Maravelias et al., 2003). Models were trained using a back-propagation algorithm (Guo and Liu, 2010).

We also used Classification Trees (CT), which partition the response variable into increasingly pure binary subsets with splits and stop criterion (De'ath and Fabricius, 2000). The result was an average across 10 Classification Trees iterations of the model algorithm.

Finally, the Maximum entropy method (Maxent) estimates a probability distribution of a species being present by maximising entropy: it seeks the most spread out distribution in space, given a set of constraints (Phillips et al., 2006). Maxent has generally a very good model performance and has been widely used for distribution models for invasive species and impacts of climate change (Stiels et al., 2011; Jimenez-Valverde et al., 2011; Murray et al., 2011; Jarnevich and Reynolds, 2011; Bradley et al., 2010; Ficetola et al., 2010; Roura-Pascual et al., 2009).

A clear limitation of modelling is that outputs are dependent on the specifically chosen input settings; in this instance, the algorithms, global climate models and scenarios of human development. To minimise potential resulting variation, we conducted consensual forecasts (Araújo and New, 2007) of combined models using the five different modelling techniques above with each of three climate models (GCMs) and two CO<sub>2</sub> emission scenarios (SRES). The purpose of consensual forecasts is to separate the signal from the “noise” associated with the errors and uncertainties of individual models, by superposing the maps based on individual model outputs. Areas where these individual maps overlap are defined as areas of “consensual prediction” (Araújo and New, 2007). This is different from averaging the individual projections, as the area predicted by the consensual forecast can be smaller than any individual forecast if there is little spatial agreement (i.e., overlap) between individual forecasts. Simple averaging across individual forecasts is considered unlikely to match the reality (Araújo and New, 2007).

The contribution of the individual models (i.e., the spatial prediction of “suitable range”) was weighted according to their AUC (Section 2.4.) in order to enhance contribution of models with higher model performance values (see Roura-Pascual et al., 2009). Only binary projections (present or absent) have been combined to generate the consensus model because continuous outputs can have different meanings for different models and cannot be simply added together (Guo and Liu, 2010). The combination of the individual forecasts then yields a projection, the consensus model, where the value of pixels vary between 0 and 1 and can be interpreted as a probability of the species being present in each pixel (Araújo and New, 2007).

The consensus model was generated using all five modelling algorithms to 6 future climatic scenarios (2CO<sub>2</sub> emission scenarios × 3 GCMs), yielding a single consensus projection for one particular time horizon. The value of the consensus model is

preferred to an average value across all models because it has two important advantages: 1/it takes into account the spatial dimension and 2/it weighs the contribution of individual models according to their predictive accuracy. An average value (and associated variability) would therefore be much less informative.

All models were run using the ModEco Platform with default parameters (Guo and Liu, 2010) and combined to consensus forecasts, weighted according to their Area Under Receiver Operator Curve (AUC) in order to enhance contribution of models with higher model performance values (see Roura-Pascual et al., 2009). The modelling process was repeated to generate consensus predictions for 2020, 2050 and 2080.

#### 2.4. Assessing suitable range and model validation

Potential habitat suitability was assessed by applying 5 different classification thresholds, whereby all pixels in which the probability of presence exceeded 0.5, 0.6, 0.7, 0.8 or 0.9 were classified as “suitable” range (Franklin, 2009). As results were similar and trend reversals could be observed under all classification thresholds, we present results obtained with a classification threshold of 0.5, which is frequently used for binary classification in the context of species distribution modelling (Franklin, 2009; Klamt et al., 2011; Nenzén and Araújo, 2011). Spatial analyses were carried out using DIVA-GIS program (Hijmans et al., 2001) and ArcGIS v. 9.3. Statistical analyses were carried out in R v. 2.15.2.

Model robustness was evaluated with AUC, which is a nonparametric threshold-independent measure of accuracy that is commonly used to evaluate species distribution models (Ward, 2007; Roura-Pascual et al., 2009; Manel et al., 1999; Pearce and Ferrier, 2000). We used the AUC because it does not depend on the classification threshold and is easily interpretable as the probability that a model discriminates correctly between presence and absence points (Pearce and Ferrier, 2000; Roura-Pascual et al., 2009). AUC values can range from 0 to 1, where a value of 0.5 can be interpreted as a random prediction. AUC between 0.5 and 0.7 are considered low (poor model performance), 0.7–0.9 moderate and >0.9 high (Franklin, 2009 and references therein). For model evaluation, the data needs to be split into a train and a test group. Here, we used 10-fold cross-validation, whereby the data had been split into 10 equal parts, with 9/10 of the observations used to build the models and the remaining 1/10 used to estimate performance; this was repeated ten times and the estimated performance measures were averaged (Franklin, 2009; Fielding and Bell, 1997). AUC values in this paper are given as mean ± SD.

#### 2.5. Assessing the trend reversal

When a trend reversal occurred in the change of suitable area, we evaluated its strength in three complementary ways (see

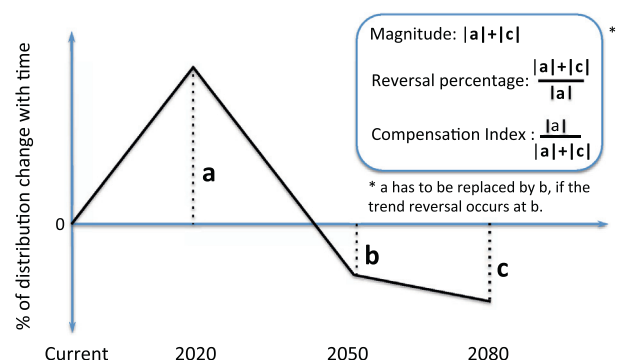


Fig. 1. Illustration of the three indices used to quantify trend changes in potential distributions.

Fig. 1). First, we calculated the magnitude of the trend reversal. The magnitude is the difference between the range size in 2080 and the date at which the trend reversal occurred (either 2020 or 2050). The magnitude of the trend reversal is expressed as a percentage of the species' current potential distribution. Second, we calculated a "reversal percentage". This is the magnitude of the reversal in any trend divided by the value of the initial trend before its reversal (i.e., the value of change in size of potential habitat at the date where the trend reversal occurred). The size of the reversal percentage reflects the "error" that one would have made if the projection had been based on an earlier date instead of 2080. Finally, in order to test whether the amplitude of the trend reversal was of the same magnitude as the initial trend, we developed a simple Compensation Index (Smaller Change/Greater Change). This index tends towards 1 when the change of the trend reversal is of the same magnitude as the initial change. In those cases, the "net" impact of climate change in 2080 on the species' range tends towards 0 (the trend is completely reversed, cancelling out the initial impact).

### 3. Results

Among the 15 species analysed, 6 showed a reversal in trend of range change over time: *M. floricola*, *M. pharaonis*, *M. rubra*, *S. invicta*, *S. richteri* and *T. albipes*. As the objective of this study is to detect potential trend reversals in potential habitat due to climate change, we present the results for these 6 species only. Although variation could be observed among different future climatic scenarios and classification thresholds, the general pattern persisted (see below). This is illustrated here for *T. albipes* (Fig. 2). There was a significant difference among projections made at different time horizons (Anova:  $F_{(1,16)} = 29.9$ ,  $p < 0.0001$ ). The trend reversal in change in range size over different time horizons was not due to an effect of the different CO<sub>2</sub> scenarios nor the different GCMs nor classification thresholds (SRES:  $F_{(1,16)} = 0.0056$ ,  $p = 0.9414$ ; GCMs: ( $F_{(1,15)} = 0.0343$ ,  $p = 0.9664$ , classification thresholds:  $F_{(1,13)} = 0.3719$ ,  $p = 0.5525$ ).

Among all 6 species and all 6 climatic scenarios that have been used at different time horizons in the future, trend reversals could be observed in total in 32 out of 36 forecasts, which is higher significantly higher than expected by chance ( $\chi^2 = 12.829$ ,  $df = 1$ ,  $p = 0.0003$ ). The same was observed using 5 different classification thresholds for consensus models of all 6 species, where 27 out of 30 projections showed a trend reversal ( $\chi^2 = 11.4286$ ,  $df = 1$ ,  $p = 0.0007$ ).

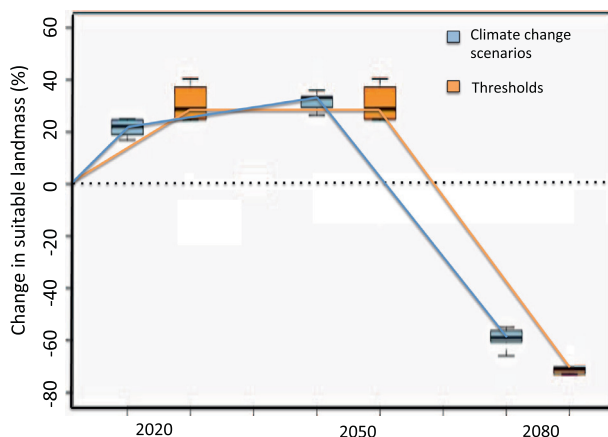


Fig. 2. Variation among projections of suitable range size for *Technomyrmex albipes* using 6 different climatic model scenarios (2CO<sub>2</sub> emission scenarios (SRES) × 3 Global Circulation Models (GCMs)) and 5 different classification thresholds (0.5, 0.6, 0.7, 0.8, 0.9).

#### 3.1. Model evaluation

Overall, model performance was good to excellent for all of the species. The mean AUC value was  $0.935 \pm 0.05$  (min 0.794; max 0.998) (Table A1 in Supplementary Online Material).

#### 3.2. Spatial predictions

The trend reversal observed in 6 species of invasive ants can be illustrated by the example of *T. albipes*, where a great initial expansion of the current potential range by 2020 is followed by a dramatic range contraction until 2080 (Fig. 3a–d).

#### 3.3. Trend reversal

In total, three species *M. floricola*, *M. pharaonis* and *T. albipes*, showed first a range expansion, which was then followed by a range contraction (Fig. 4a, b, and f). In *M. floricola*, the trend reversal was so strong that completely compensated for the initial expansion and in *T. albipes* the trend reversal even led to a decrease relative to the current potential habitat. The highest magnitude could be observed in *T. albipes*, where an initial range expansion by 36.5% in 2050 was followed by a net range contraction of –64.3% relative to the species' current potential range.

One species, *S. invicta*, showed an initial increase of 13.4% in 2020, followed by a range contraction in 2050, resulting in a net range which was only 4.4% greater than under current climatic conditions (Fig. 4d). This was then again followed by another trend reversal, leading to an increase of 35% in 2080.

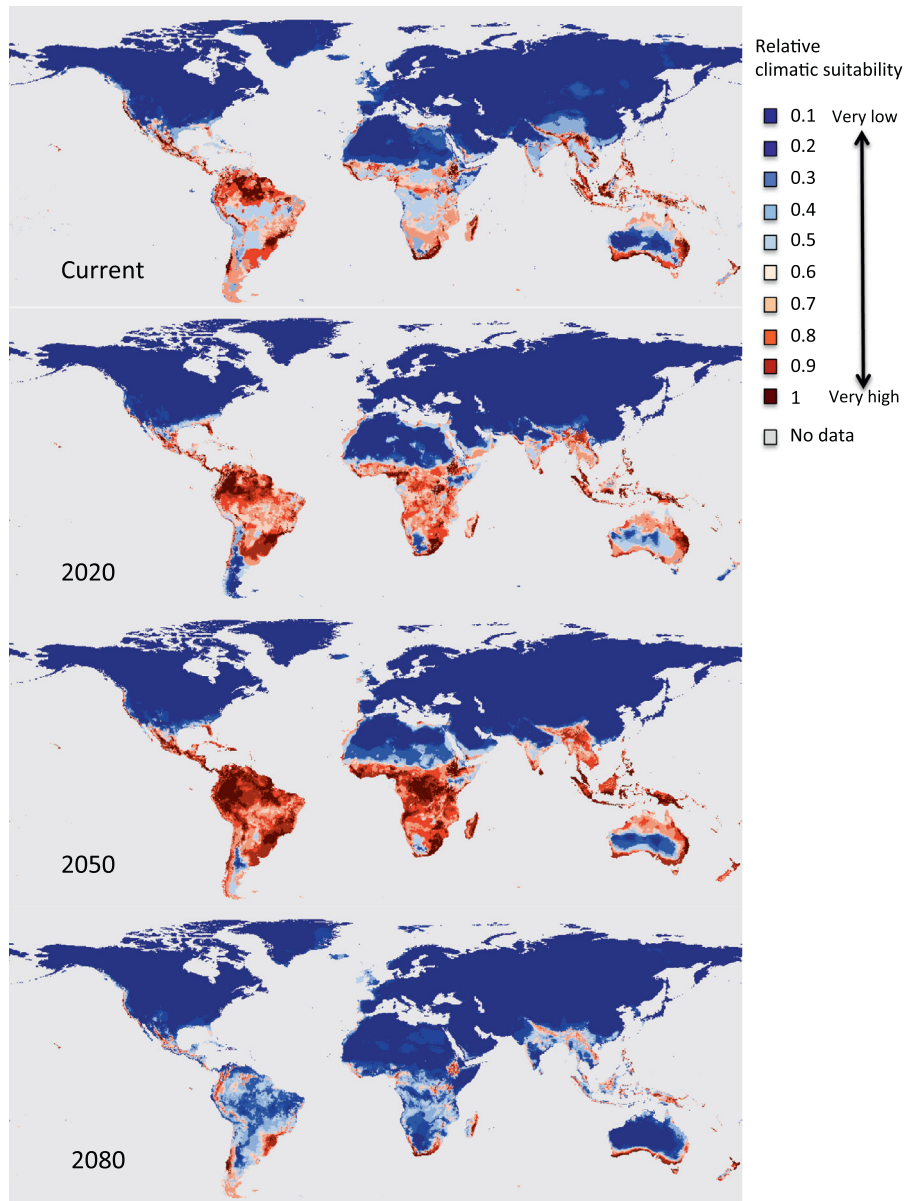
In two species, *M. rubra* and *S. richteri*, the opposite trend reversal could be observed: after the initial contraction, the potential habitat expanded (Fig. 4c and e). In *M. rubra*, the trend reversal was so strong that it eventually compensated the initial trend. In *S. richteri*, the potential habitat decreased by –10.9% in 2020, but showed subsequently expanded, leading to a net loss of only –2.3% relative to the current potential habitat. This was followed by a second trend reversal, leading to another contraction of –7.3% of currently suitable area in 2080.

Overall, in 3 species (*M. floricola*, *M. rubra* and *T. albipes*), the trend reversal changed the sign of the prediction, from an initial expansion to a subsequent contraction, or vice versa. This means that the result changed qualitatively depending on the time to which projections are made, i.e., a projection at one single time horizon produced a result opposite to that obtained by a projection to another date.

In order to evaluate the strength of these effects in the different species, we calculated the trend reversal magnitude (Fig. 5a), the reversal percentage (Fig. 5b) and a Compensation Index (Fig. 5c) for each of the six species. By far the most dramatic magnitude of trend reversal could be observed in *T. albipes* (100.8%), followed by *S. invicta* (30.6%) and *M. floricola* (12%) (Fig. 5a, dark red bars). In fact, the magnitude of the trend reversal was greater than the difference between the current potential habitat and the potential habitat in 2080 (Fig. 5a, light red bars). In other words, the net impact of climate change observed in 2080 (compared with today) was smaller than the intermediate effect, before the trend reversal. The reversal percentage reached 341% for *S. invicta* and 276% for *T. albipes* (Fig. 5b). The Compensation Index was highest for *M. rubra*, which lost –4.5% of its potential habitat in 2050, but eventually ended up with almost the same amount of habitat in 2080 as under present climatic conditions (Fig. 5c).

## 4. Discussion

The forecasts of potential distributions today, in 2020, in 2050 and in 2080 indicated a tendency to reverse over time for 6 out



**Fig. 3.** Consensual projections of potential habitat of *Technomyrmex albipes* (a) today, (b) in 2020, (c) 2050 and (d) 2080. A gradient of red colours indicates moderate (light red) to excellent (dark red) climatic suitability. Areas in blue indicate very unsuitable (dark blue) to slightly unsuitable climatic conditions (light blue).

of 15 species of the same family studied here. In 3 species (*M. floricola*, *M. rubra*, *T. albipes*), the distribution trend changes qualitatively depending on the future time horizon to which a projection is made. Where predictions at one date in the future could, for example, suggest a range expansion, projecting to another date might predict the opposite. Furthermore, there was no general pattern in the direction of the trend reversal. In 4 species an initial expansion in potential habitat was followed by a subsequent contraction while in 2 other species the opposite happened; an initial contraction was followed by a subsequent expansion. In one species an initial expansion was followed by a contraction, which was again followed by an expansion in 2080.

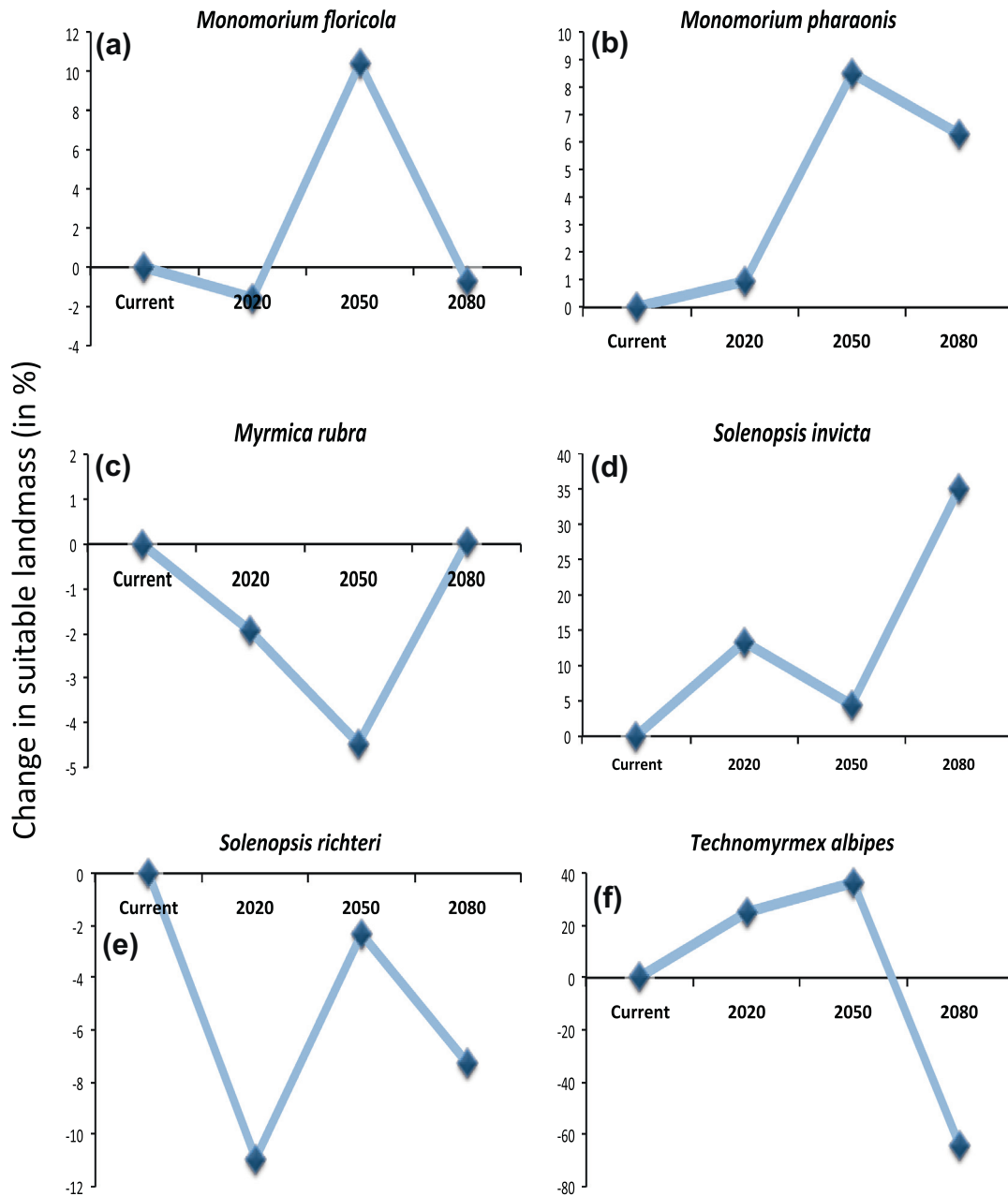
Not only are the trend reversals frequent in this rather small and homogeneous species sample (6/15), but they are also substantial. For example, between two contiguous dates, *M. rubra* shows a complete (98.9%) compensation of the initial trend, while *S. invicta* shows a percentage trend reversal of 341%. *T. albipes*

showed a trend reversal by 276% compared to the initial trend. The absolute magnitude of the trend reversal was 35% in *S. invicta* and 100.8% in *T. albipes*.

These trend reversals are unlikely to be due to “noise” in the projections as the consensus models used for predicting potential distribution showed high model performance (high AUC values, Fielding and Bell, 1997). The models were designed to include an extreme range of climate change scenarios, with an optimistic B2 and a pessimistic A2 CO<sub>2</sub> emission scenario as well as three very different and widely used global circulation models (GIEC, 2007). Uncertainty due to a single modelling method has been reduced by building models with five different algorithms that contributed to the final consensus forecast (Araújo and New, 2007). The trend reversals were not driven by a certain future climatic scenario or due to the choice of a particular classification threshold.

A possible reason for these changes in the trend of range expansions/contractions is that changes in the different climatic



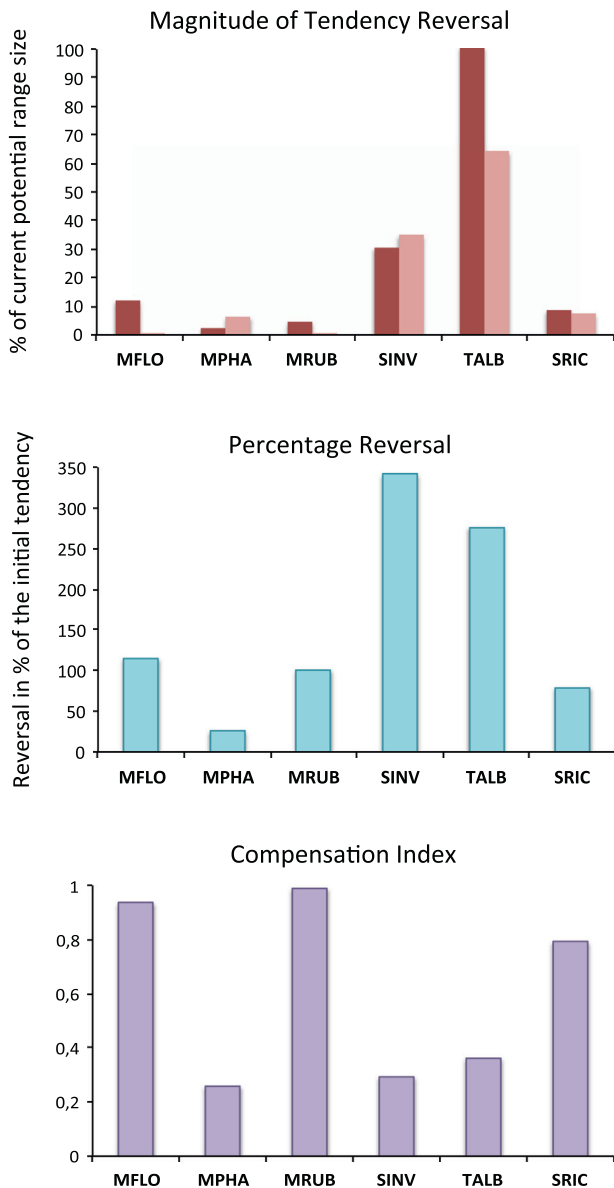


**Fig. 4.** Quantitative changes in potential habitat relative to the species' current potential range for 3 dates in the future (2020, 2050, 2080) for the six species showing trend reversals.

variables are not always correlated. For example, in some areas where temperatures rise, humidity increases, while in others humidity decreases (GIEC, 2007). Change in rainfall patterns and temperature rises are not predicted to happen at the same temporal scale across different regions of the world (Walther et al., 2002). Consequently, it is possible that some areas will become suitable at first due to changes in certain variables, increasing the total suitable area. But later in the future, other places may decrease in suitability for the species. Another, non-exclusive possibility is that the same area can first be suitable and then unsuitable for the species because a parameter optimum (e.g., temperature), has been reached and then exceeded. The fitness of ants has been shown to follow this pattern (Abril et al., 2008). Furthermore, purely “geographic” reasons may also play a role in explaining trend reversals. For example, as species niches shift in space, the total area that corresponds to the climatic conditions under which the species can

thrive may be present in a smaller amount of landmass on Earth (i.e., constrained by geographical barriers), thereby decreasing the potential habitat of the species. As the niche shifts further in space due to the changing climate so the area characterised by this set of conditions may increase again.

Previous studies using projections for several points in the future have shown data that support trend reversals in the impacts of climate change on species ranges over time (Fitzpatrick et al., 2008; O'Donnell et al., 2011). However, these studies have not explicitly pointed out that for some of the species considered a trend reversal occurred and have not discussed the potentially far-reaching consequences of these findings. For example, in the case of a threatened species, conservation decisions depend on projections of areas that will be suitable for a focal species. Similarly, management decisions for invasive species may have to be revised if trend reversals occur. It is essential to make assessments



**Fig. 5.** Quantification of the importance of the trend changes, for the six species showing change over time, for the three indices: (a) Magnitude of the trend reversal (dark red bars), expressed in % of the species current potential range. The light red bars represent the magnitude of the impact of climate change on the species potential range by 2080. (b) Reversal percentage and (c) Compensation Index. See text for explanations of the indices. In the case where two trend reversals occurred, we calculated the indices based on the trend reversal that had the greatest magnitude. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at several points in time because critical patterns might otherwise be overlooked.

For example, an invasive species might decrease substantially in 2050 but increase subsequently in 2080, reaching even a net increase in potential habitat (pattern observed in *M. rubra* in this study). If a management decision were based on a single projection in 2050, it would seem reasonable to decrease efforts of controlling the species (at least in the areas that it is not predicted to be able to invade) and direct them towards other invasive species, or other areas. However, if the decision were based on a projection in 2080, the opposite conclusion would be reached.

We also caution against the tempting conclusion that management decisions could simply be based on a single projection in the

far future (e.g., 2080). First, climatic projections for the far future (2080–2100) are considered more uncertain than medium-term projection (e.g., 2050). In addition, the successive trends of the distribution range change may be relevant. If an invasive species is predicted to decrease in 2080 but had increased in the meantime, it is possible that the impacts of the initial increase could override the subsequent decrease. Therefore, the invasive species, which has benefited from climate change at an earlier date, may still persist in 2080. Consequently, the species may still pose a greater threat compared to today – even though the model for 2080 has predicted a decline.

Similarly, a species that would be predicted to increase by 2080, might have decreased dramatically in the meantime – which could be sufficient to prevent it from occupying its increased potential distribution several decades later. A similar pattern was observed to some extent in *M. rubra* and *S. invicta*. It would be extremely worrying in the case of threatened species that could seem to be unaffected by climate change – or even benefit from it – in 2080. Indeed, an initial decrease in potential range, when it concerns an endangered species, can equate to dangerously low population sizes, or even to extinction. That the potential range subsequently increases may therefore not reflect the true impact of climate change on that species, which could be severe and underestimated.

Species distribution models have a number of limitations (Guisan and Thuiller, 2005; Sinclair et al., 2010). For example, they are based solely on climatic variables. Although climate is the most important factor determining the distribution of ants at a global scale, other variables such as biotic interactions, habitat structure and local dispersal limitations become important at a local scale (Roura-Pascual et al., 2011). In particular, it has been shown that even if climate is suitable for an invasive ant species, there is a higher chance that it invades highly disturbed sites (e.g., adjacent to roads, buildings and landscaped areas) (Fitzgerald and Gordon, 2012). Future studies on potential distributions of invasive ants may consider including these factors to get a more precise estimation of suitable areas for the species, but these forecasts will necessarily be carried out at a local scale. In this study, we have used invasive ants as a model system to demonstrate that trend reversals are a frequent phenomenon when using widely used modelling tools. Descriptive information on their spatial distributions was not the focus on this study.

It has been strongly advocated to move beyond theoretical analyses and to implement model predictions in order to protect biodiversity (Dawson et al., 2011). Notably, several hotly debated issues in conservation biology, such as assisted colonisation (Hewitt et al., 2011), triage-base assessments (Bottrill et al., 2008; Millar et al., 2007), prioritization of protected areas (Heller and Zavaleta, 2009; Summers et al., 2012) require consequential decisions if we want to mitigate the impacts of climate change on biodiversity. Although many model pitfalls have been highlighted (Sinclair et al., 2010), “trend reversals” do not seem to be recognised as a potential problem. However, it should be stressed that making predictions for additional dates (instead of a single projection in the future) comes at a marginal time cost for the modeller now that climatic projections are available. Yet, it can lead to a substantially better understanding and could even prevent disastrous consequences, if the model is to be applied for conservation or management decisions. To improve the understanding of the response of a particular species to climate change, it is even possible to choose more than three dates as there are now climate scenarios available for every decade (GIEC, 2007). This would allow quantifying the rate of trend reversal, leading to a better understanding of the response of a focal species to climate change. This will likely be superfluous in those species for which a continuous trends is observed with time, but we have shown here with a sample of 15

species of restricted taxonomy and ecology breadth that many species could be incorrectly assessed with only one date in the future.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.07.038>.

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Chapter 10 - Trend Reversal

	<i>M. floricola</i>	<i>M. pharaonis</i>	<i>M. rubra</i>	<i>S. invicta</i>	<i>S. richteri</i>	<i>T. albipes</i>
Annual Mean Temperature	x	x			x	
Mean Diurnal Range	x	x	x		x	x
Isothermality	x			x	x	x
Temperature Seasonality						
Max Temperature of Warmest Month		x	x			x
Min Temperature of Coldest Month						
Temperature Annual Range	x	x	x			
Mean Temperature of Wettest Quarter	x		x	x		
Mean Temperature of Driest Quarter					x	
Mean Temperature of Warmest Quarter						
Mean Temperature of Coldest Quarter			x	x		x
Annual Precipitation						
Precipitation of Wettest Month						
Precipitation of Driest Month			x	x	x	
Precipitation Seasonality						
Precipitation of Wettest Quarter						
Precipitation of Driest Quarter						
Precipitation of Warmest Quarter	x	x		x	x	x
Precipitation of Coldest Quarter		x		x		x

S1

Algorithm	<i>M. floricola</i>	<i>M. pharaonis</i>	<i>M. rubra</i>	<i>S. invicta</i>	<i>S. richteri</i>	<i>T. albipes</i>
SVM1	0.923	0.794	0.879	0.868	0.946	0.819
SVM2	0.975	0.914	0.922	0.958	0.985	0.928
ANN	0.972	0.960	0.933	0.954	0.974	0.961
Maxent	0.963	0.998	0.978	0.974	0.992	0.962
CT	0.973	0.936	0.951	0.906	0.902	0.854

S2

Ant Occurrences: See Appendix Chapter 8

# Combining approaches to predict an ant invasion

Gloria M. Luque, Cleo Bertelsmeier and Franck Courchamp





# 11. Combining approaches

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## *Abstract*

Ants figure among the world's worst invasive species, causing major environmental and economic impacts. Climate can strongly limit the activity and local abundance of invasive ants, and therefore their potential invasion range. Consequently, global warming is thought to enable alien species to expand into regions in which they previously could not establish. Here, we present a combination of bioclimatic modelling and an experimental method to assess the potential of an ant species to establish in Northern Europe. We carried out lab and field experiments to assess the likelihood of establishment of the Argentine ant *Linepithema humile* incipient colonies northward from their current climatic niche (in Northern France), where climate is predicted to be in theory still unsuitable. As a control, we conducted the same experiments in suitable climatic conditions, both in the invaded range (in Southern Spain) and in the laboratory. In total, 123 secure, artificial nests were buried into the ground in order to assess their establishment potential in the two climatic conditions. After one month, both colony survival and brood production were significantly higher in the laboratory than in the Spanish site and both were almost null in the French site. This study shows that there is currently a low risk of successful establishment of the Argentine ant in Northern Europe due to unsuitable climatic conditions. However, these will change, and under future global warming their potential for establishment might increase.

*Keywords: Invasive ants, bioclimatic models, transplantation experiments, Linepithema humile*

## Introduction

Ants are ecological keystone species that are both abundant and widespread worldwide (Hölldobler & Wilson 1990; Lach *et al.* 2010). Some invasive ant species figure prominently among the worst invasive species worldwide, with five among the IUCN list of “100 of the world’s worst invaders” (Lowe *et al.* 2004). Invasive ants may cause major environmental and economic impacts by disrupting ecosystems, posing major threats to biodiversity, damaging agricultural production, and infesting households (reviewed in Holway *et al.* 2002; Lach *et al.* 2010). Currently their distribution is thought to be strongly limited by climate because ants are highly vulnerable to temperature stress and desiccation (Hölldobler & Wilson 1990; Menke *et al.* 2007). However, global warming might enable alien species to expand into regions in which they currently cannot survive and reproduce (Walther *et al.* 2009; Heller *et al.* 2008).

Given the importance of ecological and economic damages of invasive ants, it becomes crucial to determine the areas of potential invasions by these problematic species. In addition, any such theoretical prediction needs empirical testing and validation. Indeed, the use of experimental approaches to better predict the effects of climate change has been strongly recommended, especially if they could be combined with theoretical studies (Bellard *et al.*, 2012). In particular, field experimental approaches in natural conditions are needed, as they account for biotic interactions, factors that are seldom considered in bioclimatic models, the main tool of theoretical predictions of climate change (Pereira *et al.*, 2012). In addition, ants provide the possibility of doing short-term experiments to assess the success of establishment, a critical stage in the success of invasions, which is a powerful approach to confirm or infirm theoretical projections.

Here, we provide such a combination of theoretical and experimental approaches – both in the lab and in the field – to assess the potential of invasion of an invasive ant species in a region where it is currently absent. We first provide current and future potential distribution maps obtained through the state of the art of bioclimatic models. We then used an innovative design of transplantation experiments to test the establishment potential of ant colonies in areas that are deemed suitable by the models, as well as in areas currently unsuitable but that are predicted to become suitable in the future, following climate change.

We focused on one of the best-known and widespread invasive species, the Argentine ant *Linepithema humile*, which is native to the subtropical riparian systems in eastern South America. This species has been introduced globally by humans and has been particularly successful in many of the world’s Mediterranean-type ecosystems (e.g., Krushelnycky *et al.* 2010; Vogel *et al.* 2010) and is listed in the “100 of the worst invaders”. This is one of the most studied species (e.g., Hartley *et al.*, 2010), in particular with several pioneering modelling studies (e.g., Roura-Pascual *et al.* 2004; 2006; 2008; 2009; 2011), which results can thus be compared to ours, for an independent test of robustness.

Following the result of our theoretical predictions, we planted artificial nests of *L. humile* for one month in an orchard in two sites, one where climate is currently unsuitable but should improve for this species, and one close to an invasion front. According to climate change models, the colony establishment should fail in the former and succeed in the currently suitable site. Establishment in that suitable site would however imply future establishment in the currently uninvaded site, once the climate has warmed there.

## Materials and Methods

### Bioclimatic models

In order to model the species potential habitat, we use ecological niche models (ENMs), which explain the species’ distribution with a set of climatic predictor variables. Several studies have used distribution models to examine changes in the geographic range of invasive ant species

considering future scenarios of climate change (e.g., Zavaleta and Royval 2002; Roura-Pascual & 2004; Levia and Frost 2004; Morrison et al. 2005; Hartley et al., 2010). Moreover, climate has been shown to be one of the most important factors determining invasion success of this species (Roura-Pascual, 2011).

### 2.1.1. Species distribution data

In total, 519 occurrence records were used from the literature, researchers, government agencies, student projects and private collectors, compiled by a public database for ant distributions (Harris and Rees 2004). We have removed points, which are clearly outside the species' climatic niche and are very likely to be either spurious records or based on indoor locations (see Figure S1 in Supplementary Online Material). For models requiring absence data (see below), 10,000 randomly chosen pseudo-absence points were generated from all around the world to provide background data.

### 2.1.2. Climatic predictors

We modelled the species niche based on the 19 bioclimatic variables provided by the Worldclim database (Hijmans et al. 2005). The full set of bioclimatic variables was used as model input because the machine learning methods used for niche modelling implicitly deal with variable selection and are unlikely to be improved – and may even be degraded by external modelling methods to pre-select variables (Elith et al. 2011, Guyon & Elisseeff, 2003, Elith et al. 2006). We used a spatial resolution of 10 arcmin (approx. 18.5x18.5 km pixel).

Future climatic data was provided by the 4<sup>th</sup> IPCC assessment report (GIEC 2007), with a time horizon at 2050. The projections are calibrated and statistically downscaled using the WorldClim data for 'current' conditions and therefore the projections can be compared. We modelled the species' potential future distribution based on downscaled climate data from 3 different Global Circulation Models (CCCMA-GCM2, CSIRO-MK2 and HCCPR-HADCM3) and 2 different CO<sub>2</sub> emission scenarios (B2a and A2a scenario, GIEC 2007).

### 2.1.3. Ecological Niche Modelling

Five different machine learning modelling techniques were used to generate the ensemble forecasts. All models were run using the ModEco Platform with default parameters (Guo and Liu 2010). The first two models use a new generation of learning algorithms: Support Vector Machines (SVMs) (Cristianini and Schölkopf 2002, Guo et al. 2005), 1-class-SVMs and 2-class-SVMS. In addition, we used Artificial Neural Networks (Franklin 2010), Classification Trees averaged over 10 iterations (De'ath and Fabricius 2000) and Maxent (Phillips et al. 2006).

The different modelling techniques, CO<sub>2</sub> emission scenarios and Global Circulation Models are used in different combinations in order to obtain a range of possible habitat maps. In a second step, the individual models were combined into consensus models reducing uncertainties of each of the models. The consensus model is constructed by superposing the maps based on individual model outputs. Areas where these individual maps overlap, are defined as areas of "consensual prediction" (Araújo and New 2007). The individual model outputs (i.e. the probability of presence in each pixel (18.5 x 18.5 km)) were weighed according to their AUC in order to enhance contribution of models with higher model performance values (see Roura-Pascual et al. 2009). We obtained a continuous projection of the consensus model with a probability of the species being present assigned to each pixel.

#### 2.1.4. Model validation

Model robustness has been evaluated with the classic AUC of the ROC curve (Pearce and Ferrier 2000), sensitivity (proportion of correctly classified presences), specificity (proportion of correctly classified absences), overall accuracy (proportion correctly classified presences and absences) and Cohen's Kappa (Fielding and Bell 1997). More details about the modelling techniques used here can be found in Bertelsmeier et al. (in press).

### Field and Laboratory Experiments

#### 2.2.1 Ant collection

Ants were collected for the experimental parts from a supercolony in a Mediterranean riparian forest in Córdoba (Spain). Ant collection was carried out in January 2010 to set up laboratory colonies and then again in May 2010 to collect the ants to set up the field colonies. We separated precise numbers of queens and workers (see experimental design below) and placed them in independent experimental colonies in the laboratory. Initial colonies never contained any kind of brood. Experimental colonies were then allocated to one of three treatments: field site in Southern Spain, field site in Northern France and laboratory conditions.

#### 2.2.2 Experimental nests

Laboratory colonies were placed into plastic boxes (foraging box) of 18x12x7 cm with plaster at the bottom. These boxes were connected to two nest tubes (1cm diameter cm and 10 cm long). Queens and brood were always inside these nest tubes. Ants were reared on a diet of 8% sugar water and a protein-based food (standardized diet, Dussutour and Simpson 2008). One month after the initiation of the artificial nests, individuals alive and brood produced (number of eggs, larvae and pupae) were recorded.

Field colonies consisted of a plastic box (9x6x5 cm) with a metallic mesh fused on the top and bottom. The bottom mesh served to prevent humidity stagnation or excessive condensation. The cell diameter of the mesh was 0,8 mm, which was large enough for workers to pass through but too small to allow passage of queens. Some soil (1/3 of the box) was introduced before closing and burying the box at 5 cm depth. A flat brick was placed on the soil surface to preserve humidity.

#### 2.2.3 Experimental area description

The geographic areas of our two field sites were selected following the results of the bioclimatic models. The first site, in climatically suitable area, was selected in Southern Spain, close to an actual front of invasion. The second site, in an area that is currently unsuitable for Argentine ants, but that will become so by 2050 under a scenario of climate change, was selected in Northern France.

The two sites were also selected so as to be as similar as possible in all other regards (habitat, humidity, openness, resource availability). The field site in Southern Spain was situated in a private land in Córdoba 6km from an area invaded by the Argentine ant. The site was chosen according to its similarity to the area where ants were collected. A river crossed the area with vegetation composed by typical Mediterranean riparian tree and shrub species. Colonies were placed approximately 5 to 10 meters from the stream, similarly to the area where they were collected (optimal microclimate for the Argentine ant, Holway et al. 2002) at the base of trees or shrubs and with a 3 to 5m distance between each other.

The field site in Northern France was also a private land: colonies were buried in an apple orchard bordered by a river, each one at a tree bottom with grass, evenly spaced by 5 meters. The orchard was in a fenced and locked enclosure and we had exclusive access during the experiment. The order in which the nests were placed in the orchard was randomized.

#### 2.2.4 Experimental design

In the laboratory we established 72 experimental colonies under optimal conditions of food (*ad libitum*) and temperature ( $24 \pm 2^\circ\text{C}$ ). In order to ensure success of establishment, we varied the initial size of the nests, in terms of the numbers of both queens and workers, aiming at including the optimal combinations for establishment (still unknown in natural conditions) as well as the suggested minimal size for establishment of this species (Hee et al., 2000). We used a complete two-way factorial design (Table 1). The same experimental design was intended for the field experiments, but due to difficulties of finding enough queens, the number of replicates had to be reduced and we used between 4 to 6 replicates per treatment. However, to compensate for harsher conditions in the field, we also used an additional category, with 6 queens and 3000 workers.

We chose to conduct the experiment in the most favourable months (in summer rather than in winter) for two reasons. First, colonies are generally much less active during winter, which would potentially mask any effect we would aim at studying here. Second, if establishment constraints were to be highlighted even during the most favourable months in Northern France, our experiment would be both sufficient and potent in demonstrating climatic unsuitability, as such effects would be only stronger in winter. Conducting our experiment in summer therefore provides us with a conservative result.

Thus, 42 field colonies were buried in Southern Spain from 8<sup>th</sup> of May to 11<sup>th</sup> of June 2010. A second set of colonies was then buried from 13<sup>th</sup> of June to 13<sup>th</sup> of July (1 queen and 10, 30, and 300 workers, five replicates each; 6 queens and 3000 workers, four replicates), making a total of 61 colonies for the field site in Southern Spain (Table 1). In Southern France, 60 colonies were buried from 22<sup>th</sup> of May to 21<sup>th</sup> of June 2010. Two more colonies with the biggest size (6 queens and 3000 workers) were buried from 28<sup>th</sup> of June 2010 to 28<sup>th</sup> of July 2010. Temperature data loggers were buried at both sites during the whole period.

#### 2.2.5 Colony collection

After one month, all colonies were unburied and the number of individuals alive was recorded. This was done in the morning (from 8am to 10am) to ensure that most of the workers were in the nest or in the close surroundings. The nest, and the soil around it, was excavated. We recorded the number of workers, queens and brood (if any) under the binocular microscope. Colonies were considered alive when they had at least one queen alive (alive queens were always found with workers). After collecting the field colonies, we placed 20 pitfall traps (cups with a diameter of 5.5 cm) in both field sites for 48h to characterize the native ant community. A visual prospection of the area was also carried out the following days to ensure that there were no more workers of the Argentine ant. A combination of pitfall traps and visual prospection has been shown to be the best method for sampling ants in aboveground ant communities (Agosti et al. 2000; King and Porter 2005).

#### 2.2.6 Biosecurity

As biosecurity is of major concern for studying biological invasions, we designed a tailored setting that prevented establishment outside the artificial nests. Pioneer attempts at using buried artificial ant colonies in the field for experiments allowed queens to leave the nest (Adams and Tschinkel 1995). Recently, Sagata and Lester (2009) used experimental nests with small-drilled

holes that did not allow queens to go outside the nests but only workers. We followed this new impetus and developed an improved design (see above), by using a metallic grid on both top and bottom sides of the nests. This setting allows a better flow of humidity in and out of the artificial nest without water accumulation. In addition, the grid size used allowed only workers to go in and out the experimental nests, preventing the passage of the larger queens. Thus, queens, which are the only reproductive, remain enclosed and can be retrieved after the experiments. However, there is a small possibility that the workers may take the brood produced out of the nests (if any) and form queenless units of workers with some brood. Although it has been shown that queenless workers can in some conditions rear sexuals (Passera et al. 1988; Vargo and Passera 1992; Aron 2001), they had to be provided with a great amount of brood (e.g. 200-300 larvae minimum) coming from big mature colonies. This differs radically from the conditions in our field experiments where no brood was provided and at least one queen was in the nest. Therefore the workers would only have the possibility to leave our experimental nests with the brood produced during the first month from our small experimental nests. However, even among our laboratory colonies, none produced many larvae or any sexuals in the first month (max. 24 larvae in the biggest nests). In fact, the first generations are dedicated to the production of new workers and colonies need to achieve a certain size and maturity to produce the first sexuals (Hölldobler and Wilson 1990).

In addition, we conducted surveys after the end of the experiment at both field sites to confirm Argentine ant absence. We also conducted an additional survey one full year later in the Northern France site. Visual searches and pitfall trap arrays confirmed the lack of Argentine ant establishment, confirming that our safety precautions have been efficient.

Values in this paper are given as mean  $\pm$  SE. All statistical analyses were performed using IBM SPSS Statistics 18 software.

## Results

### Models

Models achieved good to excellent performance with AUC ranging from 0.89 to 0.98 and Kappa ranging 0.43 to 0.63. That indicates overall a good to very good ability to predict the species presence (Table S1, Electronic Supplementary Material).

#### 3.1.1 Current potential habitat

Under the current climate, the ensemble forecast model predicts that 12.71% of worldwide landmass presents favourable climatic conditions potentially allowing the species to establish, with 2.58 % of total landmass presenting low suitability, 2.89 % medium, 1.75 % high, 2.51 % very high and 2.98 % excellent suitability. We do not provide detailed results at the world scale, since similar studies have provided global distributions (Roura-Pascual, et al., 2004), and instead we focus on Europe, for which detailed data at this scale is lacking insofar. At the scale of Europe, as much as 34% of the landmass is currently favourable for the Argentine ants, mostly around the Mediterranean Sea (see Figure 1a). Currently the species is already established in a significant part of the favourable area. However, our model shows that it could expand much further, especially in the regions that present a high percentage of climatically favourable landmass (Figure 1a).

#### 3.1.2. Favourable habitat following climate change

Surprisingly, and contrarily to the current view that climate change will favour the spread of invasive species (Bradley et al., 2009; 2010; Walther et al., 2009), the amount of potential habitat of the Argentine ant is predicted to decrease enormously by 2050. The overall decrease of

future potential habitat relative to the current potential habitat reaches 45% in the overall consensus model that combines forecasts under both the A2 and the B2 scenarios. In other words, the worldwide amount of suitable habitat of the Argentine ant should be almost halved following global change. At the European scale, the decrease is much lower, but one can observe a large shift northward in the area of suitable climate conditions, with suitability of Southern Europe decreasing much, while suitability of Northern Europe (except Scandinavia) increases much (Figure 1b). Notably, many areas in Southern Europe that are currently climatically favourable for the Argentine ant (e.g., Spain) are predicted to become unsuitable or less suitable by 2050. Conversely, large parts of Northern Europe that currently have unfavourable climatic conditions (e.g., France) will in theory become highly suitable by 2050. It is noteworthy that our models are in very good qualitative agreement with the results of previous work on this species, both for the current and the future potential distributions (Roura-Pascual, et al., 2004).

Consequently, we chose the first site in the area of current high suitability (near Cordoba, Spain) and the second site in the area of current unsuitability and future high suitability (near Paris, France, see Figure 1b). Our working hypothesis is that ant colony establishment should succeed in Spain and fail in France, if climate is currently limiting the distribution of this invasive species, as is currently thought (and shown by our models). In that case, we postulate that Argentine ant could in the future establish in the current, unsuitable area in France, following the climatic shift associated with global climate change.

## Field and Laboratory Experiments

### Temperature in the two sites

Exceptionally, temperatures in Spain were much lower than average during the field experiment, resulting in mean daily temperature not much higher in Southern Spain field site ( $18.62 \pm 0.39^\circ\text{C}$ ) than in Northern France ( $17.17 \pm 0.39^\circ\text{C}$ ) over the two months period (Mann-Whitney  $U = 1218$ ;  $Z = -2.03$ ;  $P = 0.42$ ). However, mean daily temperature is generally considered of secondary importance for ants, maximum and minimum temperature being biologically more significant (ref). Comfortingly, the difference in maximum temperature between the two field sites was highly significant, with maximum temperatures in Southern Spain being over  $3^\circ\text{C}$  higher ( $21.78 \pm 0.45^\circ\text{C}$ ) than in Northern France ( $18.70 \pm 0.45^\circ\text{C}$ ; Mann-Whitney  $U = 830$ ;  $Z = -4.29$ ;  $P < 0.001$ ). This corresponds to a medium scenario of increased global temperature for 2100 (IPCC4, 2007).

### Survival

All laboratory colonies were alive after one month, whereas only 26.2% of colonies survived the same period in Southern Spain and only 1.6% in Northern France, which was significantly different,  $\chi^2 (2, N = 195) = 143.46$ ,  $P < 0.001$ . Of note, the only colony that survived one month in Northern France had very few individuals (see below) and was extinct one week after.

We also examined differences in the number of workers per surviving nest in the two sites and in the lab (Figure 2). Laboratory colonies had an average of  $88 \pm 0.01\%$  ( $N=72$ ) workers surviving, which was significantly higher than the  $14 \pm 04\%$  workers surviving in colonies in Spain ( $N=15$ ) (Mean rank was 51 and 8 for the laboratory and colonies in Spain, respectively, Mann-Whitney  $U = 2$ ;  $Z = -6.074$ ;  $P < 0.001$ ). Queen survival was also significantly higher in the laboratory, with  $96 \pm 0.01\%$  ( $N=70$ ), than in Southern Spain, with  $76 \pm 08\%$  ( $N=18$ ), (Mean rank was 47 and 34 for the laboratory and colonies in Spain, respectively, Mann-Whitney  $U = 446.5$ ;  $Z = -2.756$ ;  $P < 0.006$ ). In Northern France, only one colony out of 62 survived and this colony contained only 1 queen alive out of 6 initial queens (16%), as well as 2 workers alive out of 300 (0.7%).

Finally, a logistic regression analysis was conducted to explain colony survival using three predictors: experimental site (laboratory, Cordoba, and France) and colony size (number of



workers and number of queens). The logistic model was statistically significant  $\chi^2_{(4)} = 191.12$ ,  $P < 0.001$  and fit well to the data (H-L goodness-of-fit  $\chi^2_{(8)} = 3.89$ ,  $P = 0.866$ ). The percentage of cases that were correctly predicted by the model increased from 54% for the null model to 92.1% for the full model. The variable site made a significant contribution to the prediction of colony survival ( $P < 0.013$ ), while colony size (either the number of workers or the number of queens) was not a significant predictor.

#### Brood produced

Almost all laboratory colonies had produced brood after one month (89%), the few that failed being among the smallest ones. In Southern Spain, only one colony had some brood present, 3 eggs and 1 larva, together with 1 queen and 2 workers (initially with 6 queens and 30 workers; Figure 3). No brood was found in colonies in Northern France. No brood was ever found outside the nesting boxes, either in Southern Spain or in Northern France.

#### Native ant communities

We recorded 13 ant species on the Southern Spain field site. The most abundant species was *Tetramorium semilaeve*, accounting for 85% presence in pitfall traps, followed by *Tapinoma nigerrimum* and *Messor barbarus*, present in 65% and 45% traps, respectively (Figure 4). The overall abundance of these ants was 1273 workers in 20 pitfall traps, 1134 of which were *T. nigerrimum*, suggesting high dominance in this community. In the field site in Northern France, we recorded only 4 species of ants. There, the most abundant species was *Myrmica scabrinodis*, present in 70% of the traps, followed by *Lasius brunneus* (55% of the traps) and *Myrmecina graminicola* and *Temnothorax recedens*, each present in 10% of the pitfall traps. Still, the overall abundance of these ants was also very low, especially compared to the Spanish site, with only 70 ants in total in the 20 traps, 46 of which being *M. scabrinodis*. Overall, ant communities in France were poorer both in species number and in abundance, suggesting a lower interspecific competition for newly establishing ants (Figure 4). The absence of Argentine ants after the field experiment could be confirmed in both sites.

#### Discussion

Our combination of modelling and experimental work, both in the lab and in the field, suggest that northern France presents currently low suitable habitat for the establishment of the Argentine ant *L. humile*.

This study first shows that *L. humile* presently could invade a very large part of the global landmass, and has already invaded a significant part of it, being now present in all continents except Antarctica. This is consistent with previous results on the potential distribution area of the species (e.g., Roura-Pascual et al. 2011). In addition, and contrarily to the current dogma of a positive synergism between climate change and biological invasions, the potential invaded areas of *L. humile* are predicted to decrease much following climate change, by almost half of the current suitable areas. This will be accompanied by a major shift northward of the favourable habitats. The decrease and global shift of the distribution of this species was also previously predicted (Roura-Pascual et al. 2011), although the very surprising result of a large global decrease was mentioned but not discussed. Of note, a decrease of *L. humile* following climate change has been recently observed over New Zealand (Cooling et al. 2011), further comforting these results.

Our study also suggests that short-term colony survival of *L. humile* incipient colonies is better in Southern Spain than in Northern France, in good accordance with climate model results. Survival in Spain field site was also lower than in the laboratory colonies. This, however, could not be only explained by climatic unsuitability, since there were colonies of *L. humile* close to the experimental area. There are two possible explanations for this result. First, the experimental

nests confined the colony to a fixed position whereas in natural conditions this species is able to move the entire colony to better or suitable nesting sites (Heller and Gordon 2006). However, this is unlikely to be the only explanation for their low survival and the lack of brood production in Spanish field site. Indeed, the survival was much higher for queens confined in the nests than for workers, suggesting that the nest conditions were suitable. There were 11 nests with at least one queen and 10 workers and these nests in the lab always produced brood. The other possible explanation of limited colony survival and brood production are limiting food resource and interspecific competition. It is in fact more likely that strong interspecific ant competition may be a limiting factor to successful establishment as both field sites were selected for their high resources availability. In the Spain field site, however, Argentine ants had to overcome the presence of many workers of at least 13 native ant species in order to survive and produce brood. Moreover, the most abundant ant species in the area, *T. nigerrimum*, has been found to outcompete the Argentine ant in encounters at food baits (Blight et al. 2010). In contrast, the Northern France site had very low interspecific competition. This suggests that the establishment of the Argentine ant in areas with low interspecific competition may be even more likely when global warming removes the first barrier of climatic conditions. In this context, future studies may choose to use bigger field colonies in order to provide an even higher propagule size and lower the effect of competition with local species. Yet, although numerical abundance and high density of workers are one of the keys to the Argentine ant success in dominating resources in invaded habitats (Walters and Mackay 2005), there is no evidence that this influenced the probability of its initial establishment in their introduced ranges. Moreover, even though the effect of propagule size has been shown to have an effect in colony performance in laboratory experiments (Hee et al. 2000; Sagata and Lester 2009), the effect of colony size under our field conditions, if any, was only secondary to the effect of site (see also Sagata and Lester 2009). It is thus likely that climate is the primary decisive factor for *L. humile* establishment, and that colony size (queen numbers and worker numbers) is also an important factor, mostly to overcome competition with local ant communities, but only in climatically suitable areas.

Our results were obtained at the cost of important efforts for biosecurity. Obviously, experimental introduction of invasive organisms outside their native range must not be conducted lightly. For this reason, we designed our protocol in order to prevent both the queens from leaving the colony (too small mesh) and the brood to develop into sexuals (too short experiment time), so that neither colony moving nor new colony foundation could be possible from our sources. Even under optimal conditions in the lab, no colony reared sexual females, although some produced males in the second month. It is known that Argentine ant colonies produce female sexuals only if they are dequeened and if no queen corpse is present in the nest because queen pheromones inhibit the development of gyne larvae (Passera et al. 1988; Vargo and Passera 1991). In our lab experiments, none of the colonies, even those of the biggest size, produced gynes when the queens died. Given that under good conditions in the lab, no queen larvae were reared, we believe that the probability of our field colonies doing so was extremely small. However, we took great care to investigate visually and with the help pitfall traps the entire experimental area, so that we could have quickly applied insecticides in the unlikely event of Argentine ants and larvae remaining in the field after the removal of the experimental nests. This innovative artificial nest technique allowed us to study experimentally the potential for establishment in new habitats under varying conditions (including in areas where the species is not invasive). Applied with the greatest care and responsibility, this technique could also be used to compare the establishment potential among different species.

To conclude, we would like to emphasize the broad significance of the experimental setting used here. With these artificial nests, many questions, ranging from behavioural to community ecology, could also be taken to an upper level of realism by using an intermediary level, between oversimplified laboratory experiments and the overwhelming complexity of field observations.

Our results also highlight the crucial importance of the combination of field and lab experiments with distribution modelling in order to account for both biotic and abiotic interactions. Finally, our approach has yielded results qualitatively different from those obtained in equivalent laboratory experiments, where it is more difficult to account for complex but crucial variables, such as the interspecific competition found in the field. Given the undisputed importance of invasive ants both in conservation and economic perspectives, and the likely exacerbation of this problem with on-going climate change, this type of approaches should be considered a potent tool for the study of biological invasions in a warming world.

### **Acknowledgments**

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**Tables***Table 1.* Two-way factorial design for laboratory and field experiments. Number of queens, workers and replicates used in each of the three experimental places.

Place	Queens	Workers			Subtotal		
		1	30	30	3000		
		0		0			
Laboratory	1	8	8	8	0	24	
	3	8	8	8	0	24	
	6	8	8	8	0	24	
	Subtotal	2	24	24	0	72	
South Spain	1	4	1	9	11	0	30
	3	5	5	5	5	0	15
	6	5	3	4	4	4	16
	Subtotal	2	17	20	20	4	61
North France	1	0	8	8	8	0	24
	3	8	8	8	8	0	24
	6	0	4	8	8	2	14
	Subtotal	1	20	24	24	0	62
		6					
			TOTAL	195			

## Figure Legends

*Figure 1.* Distribution of climatically suitable areas of *Linepitema humile* in Europe. Distribution following a consensus bioclimatic model (a) under current climate and (b) in 2080. The dots in (a) indicate occurrences of established colonies, the stars in (b) indicate the experimental sites (upper-right star is Northern France and lower-left star is Southern Spain).

*Figure 2.* Mean proportion of queens (black) and workers (grey) alive per colony after one month. Only colonies with individuals alive are considered (Laboratory: 72 colonies; Southern Spain: 15 colonies; Northern France: 1 colony). Error bars are  $\pm$  SE.

*Figure 3.* Box-plot of brood (total eggs, larvae and pupae) in colonies after one month. Outliers show that one nest in the laboratory had 257 brood and only one in Spain had brood (4 eggs). Only one nest in Southern Spain had some brood, and none in Northern France.

*Figure 4.* Number of species and abundance of the native ant communities at both sites. The bars represent the number of native workers with the number of species in each place written at the top. Both are much higher in Spain than in France, suggesting a higher competition for newly establishing species. Each colour corresponds to a different species.



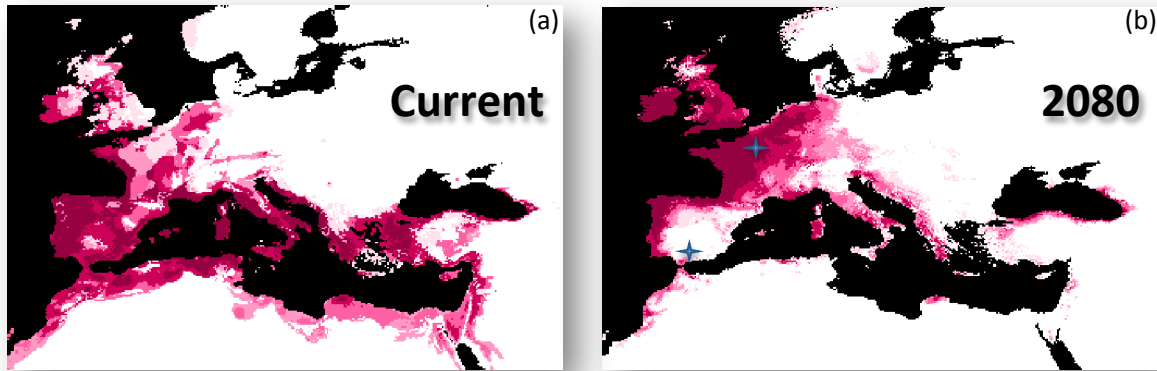


Figure 1

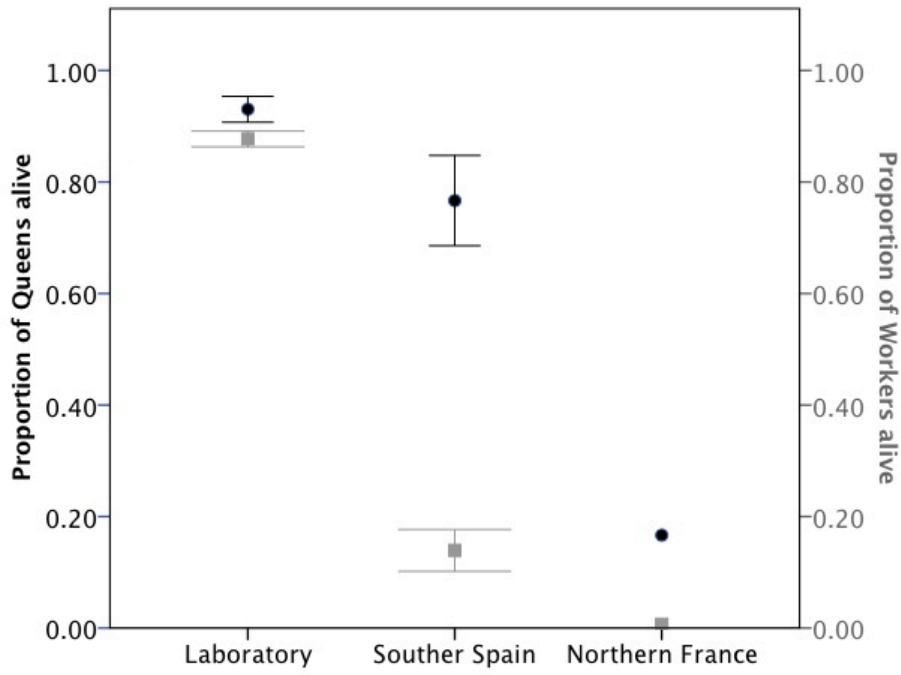


Figure 2

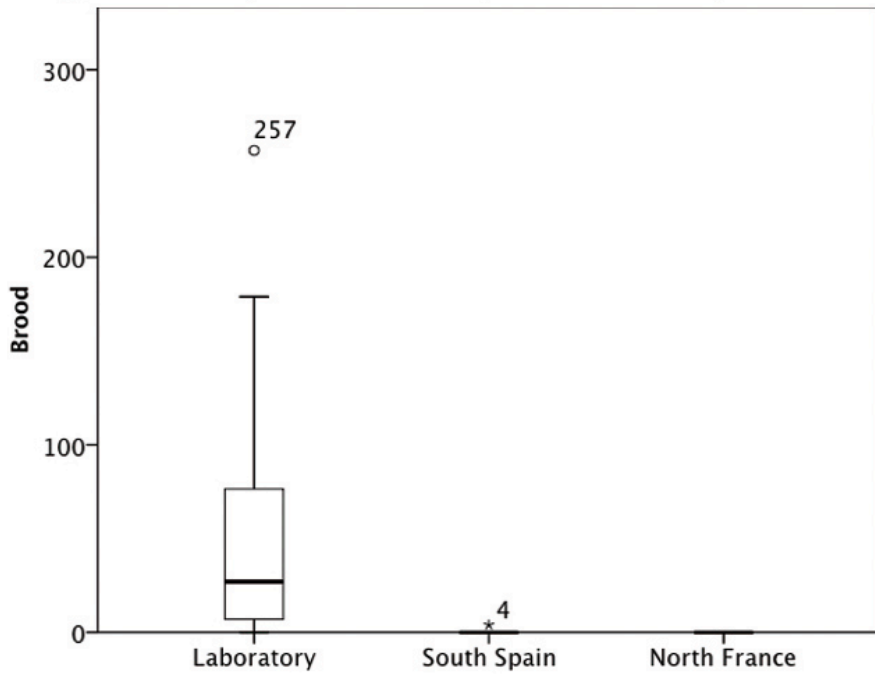


Figure 3

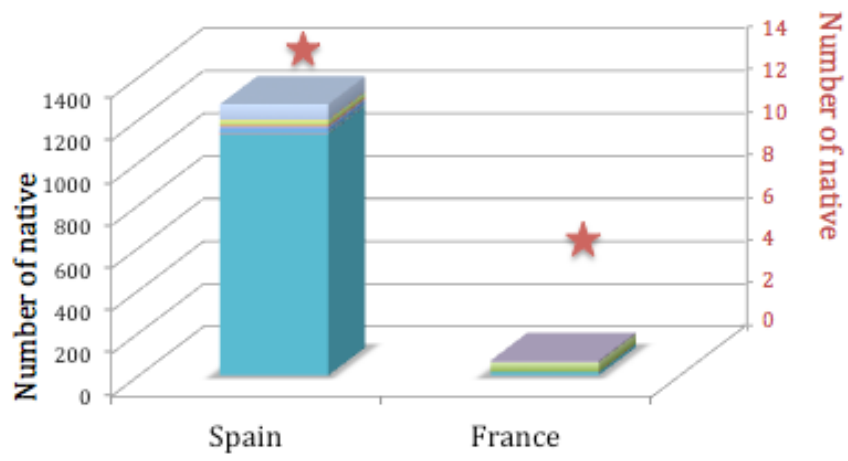


Figure 4



# Dominance hierarchy among 7 highly invasive ant species

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# 12. Dominance hierarchy among 7 highly invasive ant species

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## 1. INTRODUCTION

Biological invasions are one of the greatest threats to biodiversity <sup>1</sup>. With increased globalisation, tourism and trade, more and more species are introduced outside their native range <sup>2</sup>. Among invasive species, ants are a particularly prominent group. More than 200 exotic species have been recorded <sup>3</sup>, 19 are listed by the IUCN Invasive Species Specialist Group as highly invasive <sup>4</sup> and 5 are even on the IUCN “100 of the world’s worst invasive species” list <sup>5</sup>. Invasive ants are highly aggressive, dominant competitors and displace many native species, either through direct or indirect competition <sup>6-8</sup>. Affected taxonomic groups include most other native ants, many arthropods (spiders, crabs, insects), birds, reptiles, amphibians, mammals and plants <sup>6-8</sup>.

Studies using species distribution models have predicted suitable ranges for invasive ants, indicating that they have not yet realized their potential distribution <sup>9-12</sup>. Models indicate substantial overlaps of potential ranges of different invasive ant species (Chapter 8 & 9 <sup>13</sup>). Because invasive ants continue to be introduced into favourable yet uninvaded areas via human-mediated transportation <sup>3</sup>, these species are likely to actually arrive within these potentially suitable ranges in the future. However, invasive ants are a group of particularly aggressive species, known to displace numerous native species <sup>6,8</sup>. In addition, observations from ranges where two invasive ant species come in contact show competitive exclusion and displacement of one invasive ant by another. Examples include the mutual exclusion of *L. humile* and *S. invicta* in the Southern US <sup>14</sup>, *L. humile* and *P. megacephala* in Hawaii <sup>15</sup>, *L. humile* and *P. chinensis* in the US <sup>16</sup> and *W. auropunctata* and *P. megacephala* in New Caledonia (Hervé Jourdan, pers. comm.). It is however unclear whether there is a single ‘top’ invader and if different invasive ant species would form a dominance hierarchy.

Natural ant communities are frequently structured in dominance hierarchies <sup>17-19</sup> (but see <sup>20</sup>). In many natural communities, interference competition can result in linear hierarchies, with the superior species excluding all other species, a pattern that is common in bees, flies, moths and birds (<sup>19</sup> and references therein). Such a dominance hierarchy provides a theoretical framework, which allows predictions of locally probable and improbable species pairs <sup>19</sup>.

Invasive ants share many ecological and life-history traits, often referred to as the “invasive syndrome” <sup>21</sup>. All of these species form large polygynous colonies, covering extensive territories, which they defend aggressively and they have very generalist nesting and habitat requirements <sup>6-8</sup>. Therefore, it is likely that these invasive ant species will compete for the same resources and displace one another, unlike dominant ants in native communities, which often differ from subordinates in their diet preferences <sup>22</sup>. In addition, in native communities they invade, invasive ants break interspecific trade-offs, which allow co-existence of dominant and subordinate species <sup>23-25</sup>.

Individually, each of the invasive ant species included in our study is capable of becoming numerically and behaviourally dominant and displacing native ant species.



However, it remains to be investigated which species would be behaviourally dominant when confronted with another invasive ant species, should two species be introduced simultaneously in the same area. The aim of our study was to evaluate the performance in interference competition of 7 of the world's worst invasive ant species and to investigate the "invasive syndrome", i.e. if all invasive ant species display the same stereotypic aggressive behaviour in interference competition. We conducted pairwise confrontations, testing the behaviour of each species against each of the 6 other species. This implies realizing in total 21 dyadic confrontations. Further, we aim to test whether there is a linear, transitive hierarchy in interference competition among all 7 invasive species. All 7 species are listed by the IUCN as among the worst invasive ants <sup>4</sup>: the big-headed ant (*Pheidole megacephala*), the invasive garden ant (*Lasius neglectus*), the Argentine ant (*Linepithema humile*), the little fire ant (*Wasmannia auropunctata*), the yellow crazy ant (*Anoplolepis gracilipes*), the European fire ant (*Myrmica rubra*) and the long-horned ant (*Paratrechina longicornis*). We used a classic set up for dyadic confrontations <sup>26-28</sup> to test worker dyad interactions and symmetrical group interactions.

## 2. METHODS

### *Colony collection and maintenance of laboratory colonies*

The ants were collected between March and December 2012 in New Caledonia (*A. gracilipes*, *W. auropunctata*, *P. megacephala*, *P. longicornis*), in Southern France (*L. humile* and *L. neglectus*), in French Guiana (*W. auropunctata*) and Gembloux, Belgium (*M. rubra*). Colony fragments were maintained in plastic nest containers (55x 35x 25 cm) filled with substrate from the original nesting site (soil, wood, leaves) and contained several tubes of water. The boxes were kept at  $24 \pm 2^\circ\text{C}$  with the appropriate soil moisture. The ants were fed daily with a variant of the Bhatkar diet <sup>29</sup>.

### *Behavioural assays*

#### *One-on-one*

We determined individual fighting abilities during confrontations of all possible pairs of species among the 7 invasive ant species, totalling 21 species interactions. Before conducting the one-on-one bioassays, we selected randomly one worker from each of the stock colonies and placed it in a small plastic cylinder (diameter 2.5 cm, height 3 cm) which was placed upside down in a petri dish (diameter 5.5cm, height 1.5cm) coated with Fluon® to prevent the ants from escaping. We allowed the ants to acclimatize for 2 min before removing the two tubes containing one ant each. Behavioural interactions were videotaped for 5 min and saved on a storage unit. Each of the 21 pairwise interactions was replicated 10 times. Each worker was used only once and the arena was cleaned with 70% alcohol between two trials to eliminate any pheromones. For this experiment, we used only minor workers for *Pheidole megacephala*.

We recorded the number of occurrence and the cumulative time of the following behaviours: Antennation, mandible opening, physical aggression (worker bites the opponent), chemical aggression (worker sprays formic acid or stings the opponent), being bitten, feigning death, escaping and indifference. We also recorded the final outcome (dead, injured or alive) and the fight initiator.

*Symmetrical group confrontation*

The objective of the symmetrical group bioassay was to test interference competition between pairs of species in equal groups of 10 vs 10 workers. Because *P. megacephala* is a polymorphic species, we confronted all opponent species with 1/ only minor workers of *P. megacephala* and 2/ with a group containing 1 soldier and 9 minor workers (following the proportions in <sup>27</sup>). Therefore, we had in total 27 pairwise species interactions for the symmetrical group confrontation. We randomly selected 10 workers of each species and separated them from the stock colonies. The groups were then transferred into two small cylinders coated with Fluon® and could acclimatize for 2 min in their respective cylinder. We videotaped the group confrontations for 30 min. We conducted 10 replicates for each species interaction, except some interactions involving *A. gracilipes* (6 replicates vs *L. neglectus*, 5 replicates vs *P. megacephala* without soldier, 6 replicates vs *P. megacephala* with soldier, 7 replicates vs *P. longicornis*). We recorded the number of alive, injured and dead workers every minute during the first 5 minutes and then every 5 min until 30 min, which was considered to be the end of the interaction.

*Statistical analyses*

We calculated a Survival Index (SI) for each species based on the outcome of the group confrontations, according to the formula:

$$SI = \frac{\Sigma(A+0.5I)}{N}$$

where A is the number of alive workers, I is the number of injured workers and N the total number of workers.

In addition, we calculated a Killing Index (KI) for each species based on the outcome of the group confrontations according to the formula:

$$KI = \frac{\Sigma(D+0.5I)}{N}$$

where D is the number of dead opponents, I is the number of injured opponent workers and N is the total number of workers.

In order to combine the species' ability to survive a confrontation and its ability to kill the opponent in a single index, we used a Dominance Index (DI), which takes into account both the species' survival and killing rate:

$$DI = \frac{KI}{1-SI}$$

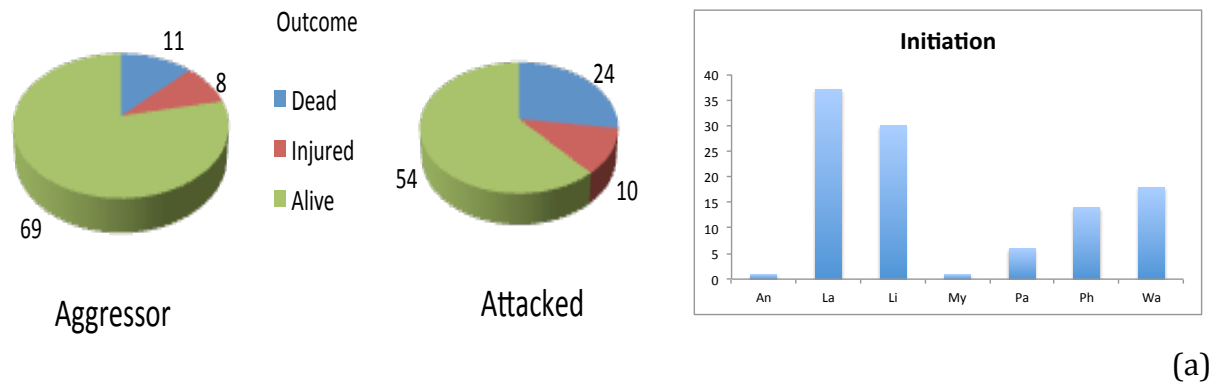
If  $DI > 1$ , the species kills more opponents than it loses its own workers and when  $DI < 1$  it has a greater death rate than killing rate.

Prior to statistical analysis of the differences in SI, KI and DI among species, we examined all data distributions using the Shapiro Wilk W test for normality. Because data did not conform to a normal distribution, we used the nonparametric Kruskal-Wallis rank sum test, adjusting for multiple comparisons with a Kruskal multiple comparison test of the `kruskalmc()` function included in the `pgirmess` package in R. We tested the relation between SI and KI using a Spearman rank correlation. All analyses were conducted with R v. 2.15.2.

We conducted a principal component analysis of the behaviours displayed during the one-on-one bioassays by the different species, using the *ade4* package in R v. 2.15.2. We tested whether the initiating a fight was associated with a certain outcome of the interaction, using a  $\chi^2$  test.

### 3. RESULTS

In one-on-one dyadic confrontations, the outcome of confrontations differed significantly according to whether the ant was the fight initiator or not, with the fight initiator winning a significantly higher proportion of fights by killing the opponent (Fig. 1) ( $\chi^2(2, 88) = 6.8801, p=0.032$ ). The analysis was conducted with the 88 interactions where the ants displayed aggressive behaviour and where it was possible to distinguish the fight initiator. The species that initiated most fights was *L. neglectus*, followed by *L. humile* and *W. auropunctata* (Fig. 1b).



(b)

Fig. 1 a) Relationship between the fight initiator and the final outcome in one-on-one confrontations, showing that species that initiated the fight more often won the confrontation, b) Species initiating fights. An= *Anoplolepis gracilipes*, La= *Lasius neglectus*, Li= *Linepithema humile*, My= *Myrmica rubra*, Pa= *Paratrechnia longicornis*, Ph= *Pheidole megacephala*, Wa= *Wasmannia auropunctata*

The differences in behaviours across species are represented by a principal component analysis showing simultaneously species and behaviours (Fig. 2). Overall, *P. megacephala* and *L. humile* are mostly associated with physical attacks and mandible opening, *L. neglectus* is mostly associated with chemical attacks and antennations, *W. auropunctata* with death feigning and *M. rubra*, *A. gracilipes* and *P. longicornis* with indifference and escaping.

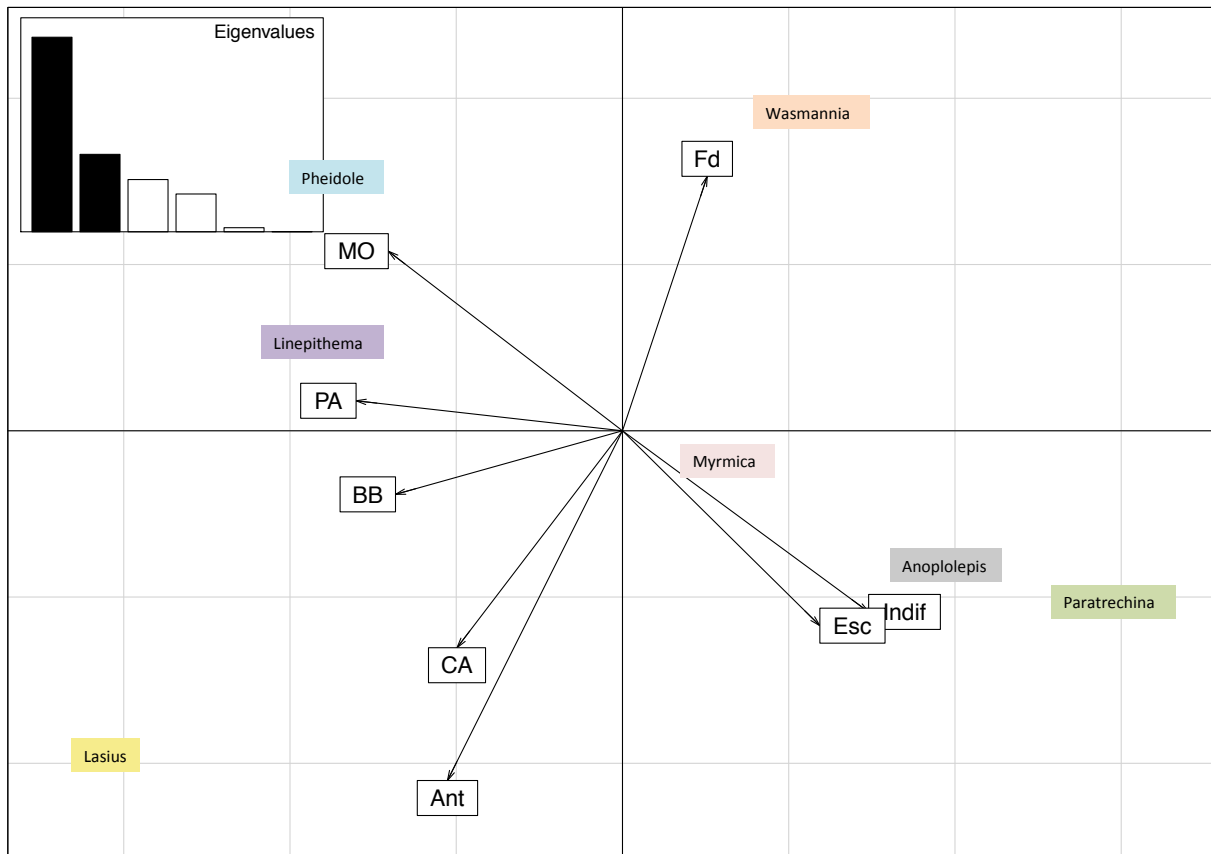


Fig. 2. PCA analysis of behaviours. Codes: MO= Mandible opening, PA= Physical aggression, BB= Being bitten, CA= Chemical aggression, Ant= Antennation, Esc= Escaping, Indif= Indifference (cumulative time), Fd=Feigning death. In all cases, except Indif, we analysed the number of times the behaviour occurred.

During group interaction of 10 vs 10 workers, we recorded the survival percentage of all species according to their opponent, and the survival percentage of that opponent after 30 min in group confrontations (Fig. 3). The lower left triangle is the survival of the focal species and the upper left triangle the survival of its opponent (which can be interpreted as the ability of the focal species to kill the opponent). For example, *M. rubra* has a very high survival in all confrontations, mostly 100% or slightly less (line 'My'), but its opponents have a very high survival, too (column 'My'), showing that the species is best at surviving but does not excel at killing its opponents. On the other hand, *W. auropunctata* has also a very high survival (line 'Wa') but its opponents have close to 0% survival (column 'Wa'), except *A. gracilipes*, *M. rubra* and *P. longicornis*. The latter three species do not dominate over *W. auropunctata* as they inflict also almost no mortality in turn. *P. megacephala* has a low survival in most pairwise and has a low killing rate, too.

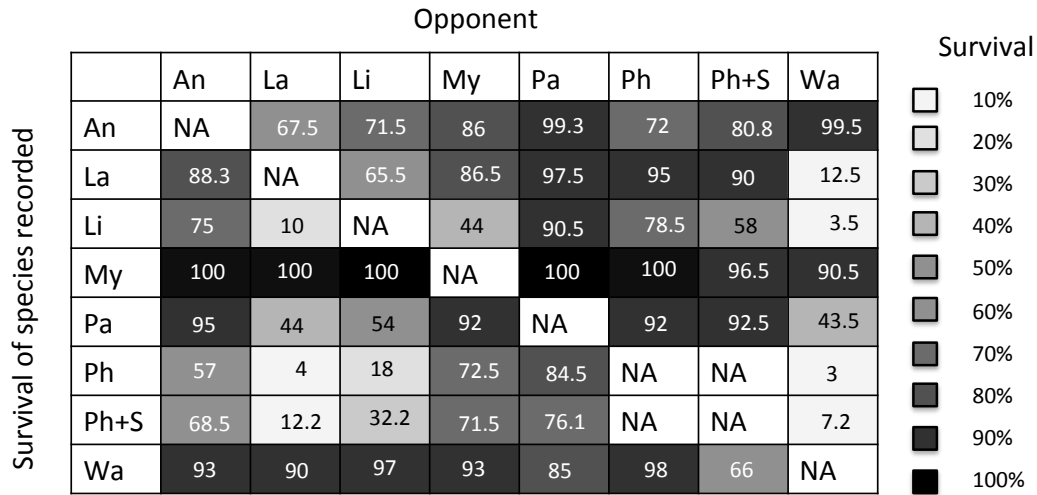
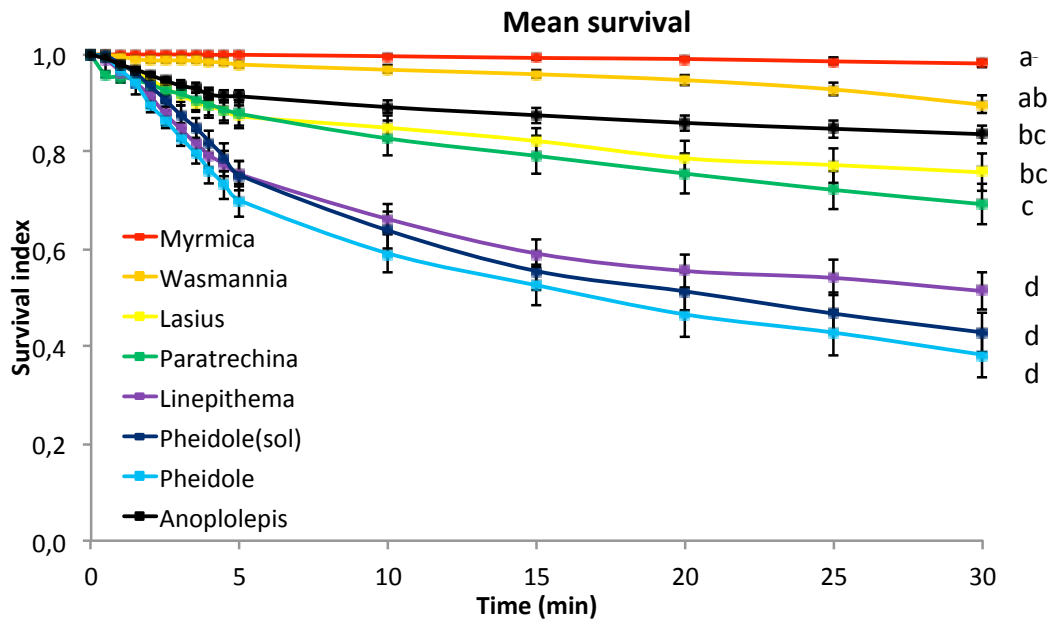


Fig. 3 Survival in pairwise group confrontations.

We summarized overall SI and KI per species across interactions (Fig. 4a+b). A Kruskal Wallis test revealed a significant difference across species, both in SI ( $\chi^2 (7) = 215.5072$ ,  $p < 0.0001$ ; Fig. 4a) and in KI ( $\chi^2 (7) = 114.8328$ ,  $p < 0.0001$ ; Fig. 4b).



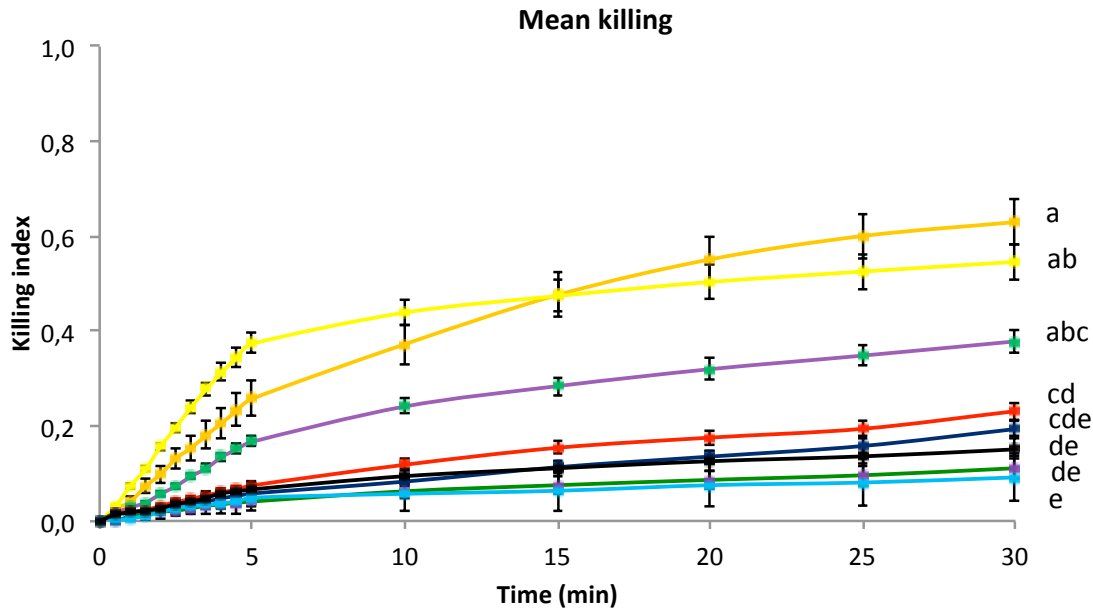
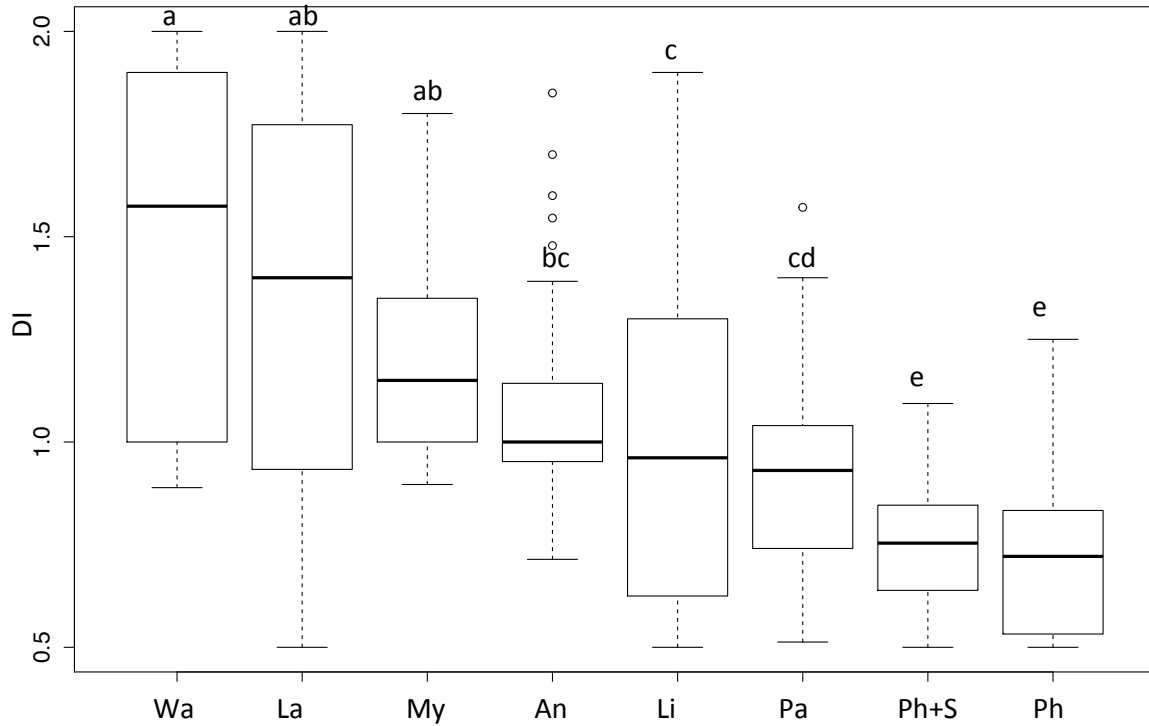


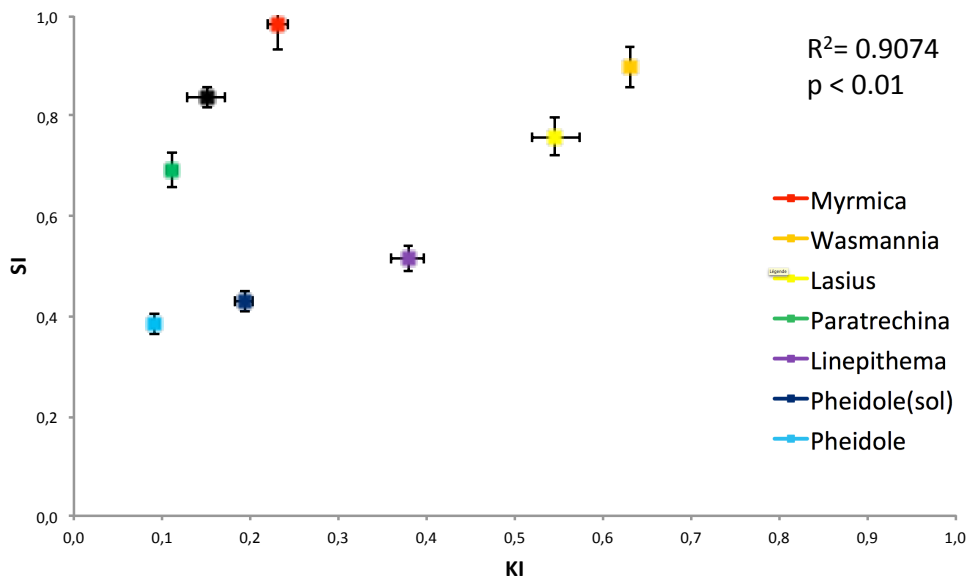
Fig. 4 (a) SI per species over 30 min of observation across interactions with different opponents (b) KI per species over 30 min of observation across interactions with different opponents. Different letters denote significant pairwise comparisons in the post-hoc multiple comparison Kruskal-Wallis test. Values are given  $\pm$  s.e.m.

We summarized the species' surviving and killing abilities in the DI index across interactions (Fig. 5a). A Kruskal Wallis test showed a significant difference in DI across species ( $\chi^2_{(7)} = 223.412$ ,  $p < 0.0001$ ; Fig. 5a).

The surviving and killing abilities are not correlated ( $r^2 = 0.1419$ ,  $p = 0.3576$ ). Thus, we also represented the species' surviving and killing abilities on two separate axes instead of summarizing them in a single index (Fig. 5b). According to the distribution of tested ants among SI and KI, the 7 species can be separated into two groups. The first group clusters at a high SI and low KI and which corresponds to the 3 species that were associated with indifference and escaping behaviour (Fig. 2): *M. rubra*, *A. gracilipes* and *P. longicornis*. The second group shows a hierarchy from species with both high KI and SI values (*W. auropunctata*) to a species with both low KI and SI values (*P. megacephala*). The latter group are species that mostly fight (associated with either physical or chemical attacks) and do not show evasive behaviour (Fig. 2). Among those 4 species, there is a significant linear relationship between KI and SI ( $r^2 = 0.9074$ ,  $p = 0.0079$ ).



a)



b)

Fig 5 a) Mean DI  $\pm$  s.d. Wa = *W. auropunctata*, La = *L. neglectus*, My = *M. rubra*, An = *A. gracilipes*, Li = *L. humile*, Pa = *P. longicornis*, Ph+S= *P. megacephala* with soldier, Ph = *P. megacephala* without soldier b) Mean SI  $\pm$  s.e.m, mean KI  $\pm$  s.e.m.

#### 4. DISCUSSION

Despite being among the worst global invaders, the 7 invasive ant species differed greatly in their performance in interference competition. The top dominant competitor was *W. auropunctata* and the least dominant species was *P. megacephala*. In addition to the quantitative difference in interference competition, there was a qualitative difference in the type of interaction between species. On the one hand, 4 species (*W. auropunctata*, *L. neglectus*, *L. humile*, *P. megacephala*) interacted aggressively with all other species and displayed behaviours such as mandible opening, chemical and physical attacks. These 4 species formed a clear linear hierarchy, with the top species excelling at inflicting injuries and causing death of its opponent, while suffering itself very low mortality, and the lowest ranking species of the four being injured and killed more frequently without being able to injure or kill as much the other species. On the other hand, the 3 remaining species (*A. gracilipes*, *P. longicornis*, *M. rubra*) mostly avoided aggressive interactions by displaying indifference or escaping their opponents. Consequently, they had a high survival rate but a low killing rate. Among these 3 species, it is difficult to establish a 'dominance hierarchy' because in pairwise interactions, the species avoided each other and death or injuries rarely occurred. But how does this evasive group relate to the linear dominance hierarchy among the other 4 species? For the purpose of interspecific comparison, different types of dominance indices exist, which rank the species according different weights to dominant (e.g. killing) or subordinate (dying) behaviour<sup>30</sup>. We have illustrated the outcome of any of these methods, using a dominance index (DI), which takes into both SI and KI. All ranking methods 'force' a ranking among all 7 species, with the 3 evasive species intercalated in the linear dominance hierarchy (Fig. 5a). However, a single ranking misses the two different strategies entirely (Fig. 5b). Ant community studies classically define the dominance score of a species as the percentage of time it initiates an attack or when its presence elicits avoidance in an encounter with another species<sup>22,31,32</sup>. Applying this definition to the 7 invasive ants species here, the 3 evasive species would be ranked lowest (Fig. 1b). Given their high overall survival and the fact that all 3 species win pairwise interactions against *P. megacephala*, this classic dominance index seems inadequate here. Under laboratory conditions, different species have also been ranked according to their mean survival in confrontations<sup>27,33</sup>. This ranking, however, would greatly advantage the 3 species of the evasive group because of their high overall survival. But this ranking does not take into account the species' rather poor attacking and killing abilities. Therefore, this appears inadequate, too, for summarizing the dominance relationships among the 7 species studied.

Behavioural differences among the 4 species in the linear hierarchy include the use of mostly physical defences by the two lowest ranking species, *P. megacephala* and *L. humile*. Surprisingly, the highest-ranking species in our study, *W. auropunctata* displayed death-feigning behaviour in interactions where it ultimately won. This is remarkable given the observation by Blight et al.<sup>26</sup> of death feigning by *L. humile* when it was losing the confrontation. A further interesting result is that the fight initiator was more likely to dominate against the opponent (fig. 1). It would be interesting to know whether this is because the winner of an interaction had some way of assessing its relative strength before engaging in a fight, which made it more likely to initiate the fight. Or, alternatively, the action of initiating a fight could give an advantage to the individual displaying this behaviour in a confrontation. Our experimental set-up does



not allow discriminating between these two hypotheses. But it would be interesting if future studies could separate the cause and the consequence of fight initiation.

In the group confrontations, different species differed remarkably fast in their mean SI and KI (fig. 4 a+b). This suggests that even a shorter observation length could be sufficient to get qualitatively similar results. An unexpected result was that the addition of a soldier to *P. megacephala* groups did not have a significant effect on their survival or killing rate. The soldier displayed a passive behaviour and did not engage preferentially in confrontations. As soldiers are bigger in size than the minors and more costly to produce for the colony, one would expect a benefit during confrontations. However this apparent lack of a soldier effect has been observed before in a native *Pheidole* species when it was confronted with *W. auropunctata* <sup>34</sup>.

Although it followed strictly what has now become classical protocols to assess interspecific dominance, our approach includes some limitations. Among them, the laboratory settings under which we carried out the confrontations may have created some unrealistic conditions. The small petri dish, which favoured a fast encounter of the two opponents and hindered escapes, may restrict the natural behaviour. In particular, species with evasive behaviour may have a lower mortality rate in the field. Confrontation experiments with two species of *Formica* have shown that dominance behaviour may be contingent on many factors such as habitat type, resource value and competitor behaviour <sup>35</sup>. In addition, the interactions took place in a 'neutral' area and the behaviour may change in the presence of an established colony. It would be interesting to carry out an experiment at the colony level with territories owned by the opponent species. Resource dispersion can also influence co-occurrence patterns <sup>36</sup>. Further, group size can affect the behaviour and efficiency of different fighting strategies <sup>28</sup>. For example, in interactions between *L. humile* and the native *Tapinoma sessile*, the result depends on the group size in symmetrical interactions. Workers of *L. humile* fight cooperatively and gain a local numerical advantage by attacking together <sup>28</sup>. In our study, it is possible that chemical attacks are the strategy most efficient at 10 vs 10 worker confrontations, while physical attacks may be advantageous in confrontations when more nestmates are present. Similarly, soldiers may need recruitment to efficiently work together and give an advantage to *P. megacephala*. Future studies might test the effect of group size on the efficiency of different fighting strategies in invasive ants. Furthermore, in the field, different environmental conditions can favour different species and it has been suggested the relative suitability can shift the dominance from one invasive species to another <sup>16</sup>. In that respect, temperature is especially important and different thermal preferences can be a more decisive factor than interference performance <sup>37,38</sup>. The seasonal variation and the current state of the reproductive cycle can also influence the aggressiveness of a given colony (<sup>35</sup> and references therein). In addition, the presence of disturbance can influence the dominance of invasive species <sup>39</sup>. Finally, biotic interactions in the invaded environment (e.g. parasites) may affect dominance hierarchies <sup>40</sup>. However, generally parasites are not introduced at the same time as the invasive species. Overall, mitigating biotic or abiotic factors have to be taken into account when making predictions for a particular area.

Generally, given the ecological similarity and their aggressiveness against native species <sup>6</sup>, the 7 invasive ant species are likely to exclude each other, or at least those that really interact in confrontation (*W. auropunctata*, *L. neglectus*, *L. humile*, *P. megacephala*). A possibility that cannot be discarded is that the 3 remaining species (*M. rubra*, *P.*

*longicornis*, *A. gracilipes*) may co-exist with each other or even with one of the more aggressive species. Co-existence of these 4 other species or the clustering into local patches dominated by different species may happen, instead of a top dominant invasive species wiping out lower ranking species. One possible mechanism would be the existence of a discovery-dominance trade-off, where species excel either at discovering resources or dominating them <sup>31</sup>, or a thermal tolerance-dominance trade-off, <sup>22,41</sup> as often observed in native communities (but see <sup>42,43</sup>). Similarly, thermophile native ants can co-exist with invasive ants <sup>44</sup>. Whether such a trade-off exists among invasive ants remains to be investigated.

One intriguing question is how the two different interference strategies that we observed can produce similar impacts on native communities. One possibility is that the 'evasive' group (*M. rubra*, *P. longicornis*, *A. gracilipes*) does not display the same behaviour towards native species. Perhaps these species are evasive only when confronted with a very aggressive invasive species and more aggressive towards native species. But this would imply that the 'evasive' species have some way of estimating the strength of their competitor. Another possibility is that the negative impacts of these species on native biodiversity are not so much due to direct interference but resource exploitation or other indirect effects.

Our study illustrates the use of complementary dominance indices, demonstrating that the complexity of dominance relationships between different invasive species would not be captured by a single summary index (such as FI, KI or DI). It also points in new research directions. Especially interesting are the two different mechanisms of invasiveness, which complements the view of invasive ants as a homogeneous group, that are supposed to success in invading by breaking the dominance-discovery trade-off in native communities <sup>24</sup>. If invasive ants have different behaviours and do not universally break the discovery-dominance trade-off, this can have consequences for management strategies. For example, it has been suggested that toxic baits have only minimal negative impacts on native ants because *L. humile* is a faster discoverer of the bait and is able to dominate it <sup>45</sup>. However, for invasive ants that do not show the same behaviour, toxic baits may have much greater impacts on non-target species.

Overall, this study questions the existence of a universal behavioural strategy as part of the 'invasive syndrome' in ants and calls for further studies on the conditions under which these different behaviours can be observed.

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# Colony-colony interactions among invasive ants

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# 13. Colony-colony interactions

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## 1. INTRODUCTION

Ants are conspicuous and dominant members of most terrestrial ecosystems and are often classified as key stone species or ecosystem engineers since they shape in large part the structure and diversity of their habitats <sup>1</sup>. Among the more than 12,000 described species of ants, more than 200 have been transported by humans and introduced outside their native range <sup>2</sup>. A subset of these exotic species has become invasive and has enormous impacts on native biodiversity, ecosystem functioning and animal or human health <sup>3-5</sup>. In addition, many species are a nuisance because they can invade houses, destroy electrical equipment and impact agriculture, causing high economic losses <sup>6</sup>. A total of 19 species has been listed as highly invasive by the IUCN invasive species specialist group <sup>7</sup> and 5 species are even on the '100 of the worst invasive species' list <sup>8</sup>. In natural ant communities, a variety of mechanisms allow co-existence between species <sup>9</sup>. In particular several trade-offs in native ant communities have been highlighted in the literature, for example the thermal tolerance-dominance trade-off, where species are either behaviourally dominant or highly tolerant to extreme temperatures, <sup>10-12</sup> and the discovery-dominance trade-off, where species excel either at discovering a food resource or at dominating it <sup>13-15</sup>. Invasive ants, on the other hand, are thought to displace native species by breaking these trade-offs, excelling both at interference competition and exploitation competition <sup>16,17</sup>. Very few native species have been shown to be able to resist the most harmful invasive ant species (e.g. <sup>18-20</sup>). Invasive ants are generally thought to be very aggressive and behaviourally dominant species. However, it remains unclear how two invasive ant species would interact should they be simultaneously introduced within the same area. Generally, in regions where multiple invasions have occurred, invasive ants do not co-exist in the same area <sup>21-23</sup>. A recent modelling study has identified large uninvaded areas that may be suitable for 15 of the most invasive ants (Chapter 8 & 9). The suitable range of several highly invasive ants overlaps substantially, creating large potential invasion "hotspots" (Chapter 8 & 9). But predictive species distribution modelling does not take into account biotic interactions <sup>24</sup>. Therefore it is primordial to investigate whether a single top dominant ant species may ultimately prevail, displacing all other aggressive, yet less competitive invasive species. Alternatively, co-existence or a mosaic of different invasive ants species may be possible. Classically, species interactions have been investigated in community studies, using pitfall traps to record the numerical dominance of different species and with baits to observe behavioural interactions <sup>9</sup>. In the case of interactions between multiple invasive ant species, this is not possible because they do not co-occur in the same areas, yet, although they may interact in the future. To circumvent this difficulty, studies have used behavioural assays under laboratory conditions, placing one or several workers of different species in a petri dish and recording their interactions <sup>18,25,26</sup>. A recent study (Chapter 12) has investigated pairwise dominance interactions among some of the most invasive ants and identified four species that behaved very aggressively towards opponents and showed a clear linear dominance hierarchy: *Wasmannia auropunctata* > *Lasius neglectus* > *Linepithema humile* > *Pheidole megacephala* (Bertelsmeier et al. in prep.). Therefore, these four species are unlikely to co-occur within the same area and the single top dominant species seemed to be *W. auropunctata*. However, these classical interference experiments in petri dishes are



based on unrealistic laboratory conditions and so far, it is unclear whether results from petri-dish experiments can be extrapolated to the whole colony. For example, the low number of workers used (either one or ten) does not allow species to display interference strategies depending on a minimum number of workers<sup>26</sup>. Further, the presence of resources or a territory is known to influence dominance hierarchies<sup>27</sup>. Clearly, experiments under more realistic conditions are needed – at the whole colony level and over a medium to long time span. Here, our aim is to study colony-level interactions between pairs of four of the worst invasive ant species in symmetrical colony interactions. To increase realism, we provided the species with sufficient space to avoid confrontations (unlike the small petri dishes) and we monitored the interaction over 6 weeks. Further, we investigated interactions and survival of all four invasive species simultaneously, reflecting a more complex scenario of multiple invasions in the same area.

## 2. METHODS

### 2.1. Colony collection and maintenance of laboratory colonies

The ants were collected between March and December 2012 in New Caledonia (*W. auropunctata*, *P. megacephala*) and in Southern France (*L. humile* and *L. neglectus*). Colony fragments were maintained in plastic nest containers (55x 35x 25 cm) filled with substrate from the original nesting site (soil, wood, leaf) and contained several tubes of water. The boxes were kept at  $24 \pm 2^\circ\text{C}$  with the appropriate soil moisture. The ants were fed daily with a variant of the Bhatkar diet<sup>28</sup>.

### 2.2. Colony-colony experiment

We tested pairwise colony interactions among four species, *W. auropunctata*, *L. neglectus*, *L. humile* and *P. megacephala* (i.e., 6 pairwise interactions). Each pairwise interaction was replicated 5 times, except the interaction *L. humile*-*L. neglectus* which was replicated 6 times. Each colony consisted of 300 workers and one queen. Colonies of *P. megacephala*, which was the only species to possess two worker castes, contained 10% soldiers and 90% minor workers (following Kirschenbaum & Grace, 2008). Each colony was placed in a foraging arena (18 x 12 x 7 cm) with a metal mesh fused to several holes on the top lid for aeration and a plaster bottom (Fig 1a). The foraging arena was connected to a nest tube (1cm in diameter and 10cm long), which was divided by a piece of cotton into a nesting space (adjacent to the foraging arena) and a water source. The nest tube was covered with a red filter in order not to disturb the ants in the nest but to be able to count individuals in the tube. The foraging arenas of interacting colonies were connected via a plastic tube “bridge”. Ants were fed *ad libitum* with a variant of the Bhatkar diet<sup>28</sup>, placed in each foraging arena. After placing the colonies in their respective arenas, they were allowed to acclimatize and move to the nesting tubes for 24h. After that, the bridge was unblocked by removing the obstructing piece of cotton, therefore allowing the interaction between the adjacent colonies. During the first hour after connection, the number of fights in both arenas (incursions) was recorded every ten minutes. Afterwards, we monitored the fights every hour over 5h. Subsequently, fighting was only rarely observed and we recorded daily the number of surviving individuals of interacting species, over 42 days.

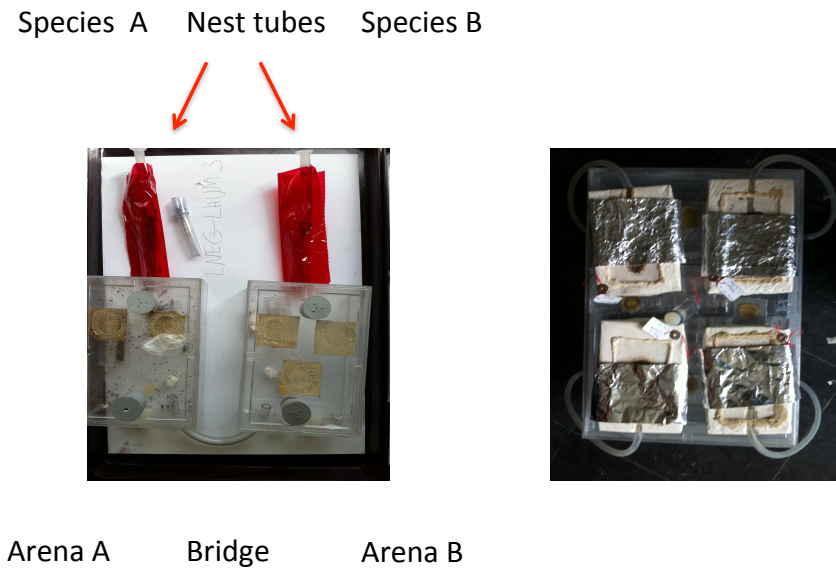


Fig. 1 Set up a) colony-colony experiment b) 4 colonies experiment

### 2.3. Four colonies experiment

We recorded the simultaneous interactions of all four species, using 4 replicates. Each colony consisting of 300 workers and two queens was placed in a plaster nest (10 x 6 x 1 cm) covered with Plexiglas. The nesting space was darkened with aluminium foil that could be removed to monitor punctually the survival of the colonies. All four plaster nests were posed on the top of a large, common foraging arena, to which it was connected with a plastic tub (diameter 0.8 cm, length 95 cm). The foraging arena (24 x 17.5 x 10 cm) contained styropor with evenly spaced holes (diameter 2.8 cm, depth 3 cm) to provide a certain level of habitat complexity and artificially increase available space. The ants were allowed to acclimatize in their respective plaster nests for 24h prior to the connection to the foraging arena. After connecting all four plaster nests, we recorded the number of fights and the identity of the opponent species every hour over 5h after connecting the nests to the foraging arena. We also recorded nest entrance blocking behaviour, whereby workers obstruct the entrance of their own nest to prevent intruders from getting into their plaster nest, and the number of workers involved in this type of behaviour during the observation periods. The complexity of habitat precluded from recording daily the number of surviving workers because the whole set-up needed to be dismantled to be certain to count all ants. Therefore, we recorded the “winner” at the end of the interaction after two weeks, i.e. the only remaining species and the number of workers surviving.

### 2.4. Data analyses

Prior to statistical analysis of the results, we examined all data distributions using the Shapiro Wilk W test for normality. Because data did not conform to a Normal distribution, we used the nonparametric Mann-Whitney test to test for differences in mean incursions in pairs of species and the Kruskal-Wallis rank sum test to compare

mean incursions across interactions (colony vs colony). We also used the Kruskal-Wallis rank sum test to compare the mean number of fights between pairs of species and the occurrences of entrance blocking behaviour among species. We used a Spearman rank correlation to relate the difference in incursions between pairs of species and the difference in mortality between pairs of species.

We modelled the survival of each colony during pairwise colony interactions, using a nonlinear model:  $n(t) = e^{-at + \log(d-p)} + p$

where  $n(t)$  is the number of surviving workers at time  $t$  and  $d$  is the initial colony size at  $t_0$ , which represents the number of workers that survived the initial confrontation during day 0 after the connection of the two adjacent arenas. The fitted function starts only one day after the beginning of the confrontation because of the discontinuity in colony size, which is due to a rapid decline after the initial fights. Therefore,  $d$  gives a measure of the number of workers lost during the first interaction.  $p$  is the asymptotic limit when  $t$  tends towards infinity. This parameter allows comparing the final colony sizes after 42 days of observation.  $a$  is the steepness of the slope, measuring the speed at which the colony size decreases.

The fitted model and the estimated parameters are represented Figure 2, using an example of the interaction between *L. humile* and *L. neglectus*. The parameters are estimated using the function `nls()` in R v.2.15.2, using the algorithm 'port' which allows constraining the values of  $d$  to 300 and the values of  $p$  to 0.

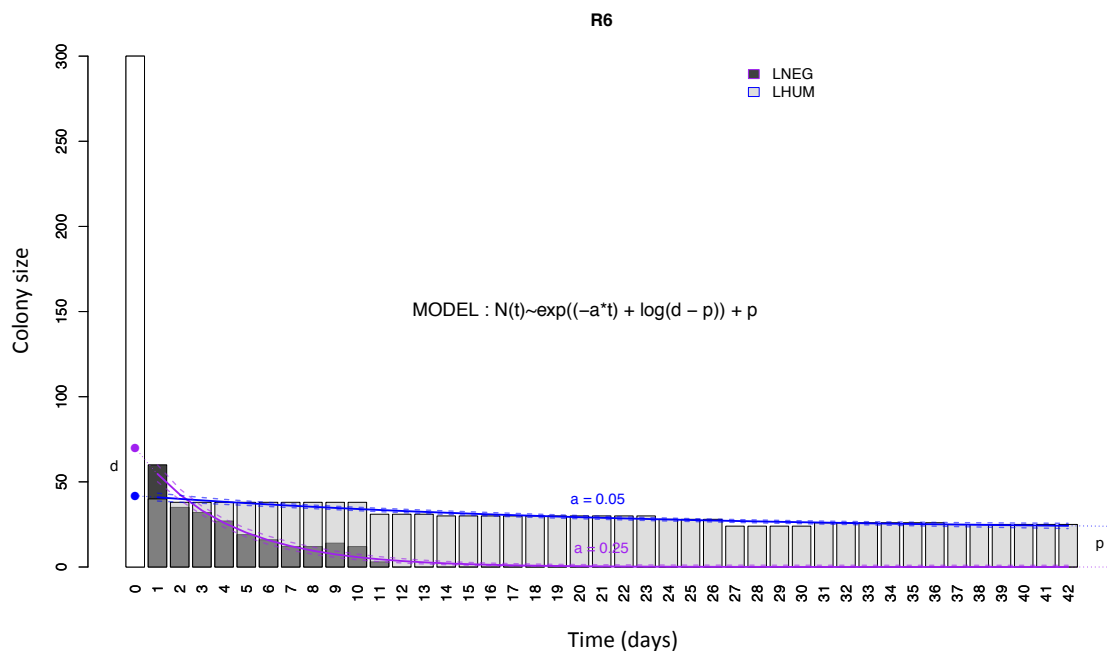


Fig. 2. Example of fitted models for the survival of two colonies in replicate 6 of the interaction *L. neglectus* against *L. humile*. The grey histogram represents the raw data (dark *L. neglectus*, light *L. humile*) and the two lines correspond to the models fitted for each species (purple *L. neglectus*, blue *L. humile*).

Based on estimations of the errors of the estimated model parameters, confidence envelopes for each model in a parameter space were calculated, following Beale (1960). For each colony, a model was fitted and the corresponding parameters  $d$ ,  $p$  and  $a$  were

estimated. To compare the performance of each species, the survival process of each colony was represented in a parameter space (a,d,p) with its corresponding confidence envelope. In order to simplify the representation, we realized the representation in 2D (plane p,d and plane a,d). Subsequently, we carried out a PCA to represent each model in a parameter space with uncorrelated axes, placing the data point of each model at the centre of gravity within its confidence ellipse. The PCA summarizes the information of the tree parameters on a two-dimensional graph in a way in an optimal way. Then, we realized a classification analysis, using the distance between points using the `hclust()` function in R. The classification analysis defines groups of colonies with similar demographic processes.

### 3. RESULTS

#### 3.1 Colony-colony interactions

During colony-colony interactions, the mean number of incursions into the arena of the opponent differed between species (Kruskal Wallis test:  $\chi^2_{(3)} = 41.2113$ ,  $p < 0.0001$  (Fig. 3a). *L. humile* performed the most incursions and *W. auropunctata* the least. Because of the differences in the number of incursions, there was a tendency for fights to take place rather in one arena than the other across all species pairs: *P. megacephala* – *L. neglectus* ( $\chi^2_{(1)} = 52.1063$ ,  $p < 0.0001$ ), *W. auropunctata* – *L. neglectus* ( $\chi^2_{(1)} = 7.0755$ ,  $p = 0.0078$ ), *L. humile* – *W. auropunctata* ( $\chi^2_{(1)} = 6.8598$ ,  $p = 0.0088$ ) and *P. megacephala* – *W. auropunctata* ( $\chi^2_{(1)} = 6.9876$ ,  $p = 0.0082$ ). The difference in the number of incursions during pairwise interactions was negatively correlated to the difference in mortality by the end of the experiment (Fig. 3c) ( $r^2 = 0.9373$ ,  $p < 0.0318$ ): the higher the species' tendency to initiate fights in the arena of its opponent, the higher its mortality.

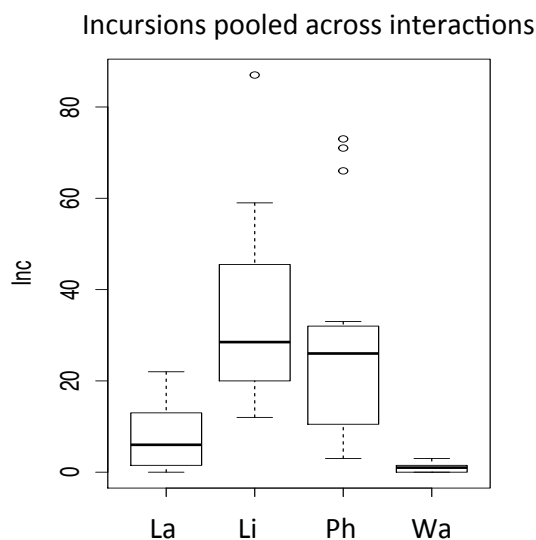


Fig. 3a Number of incursions during pairwise colony interactions pooled across all replicates

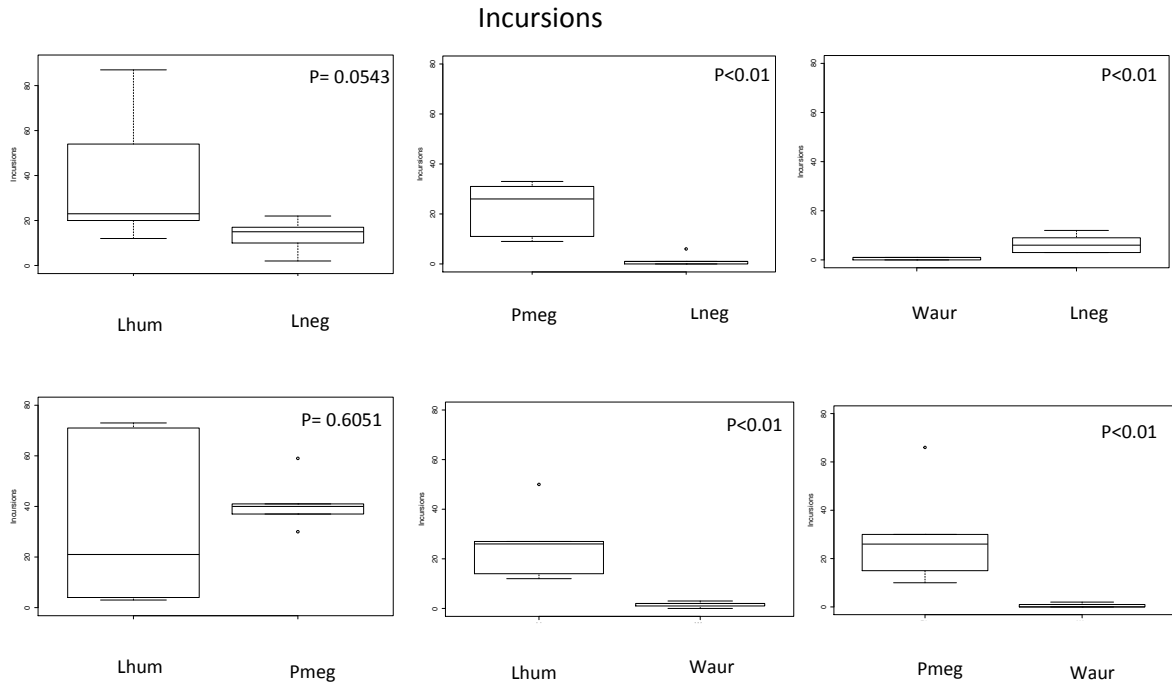


Fig. 3b Incursions into the arena of the opponent, per species combination. LNEG= *L. neglectus*, LHUM= *L. humile*, WAUR= *W. auropunctata*, PMEG= *P. megacephala*.

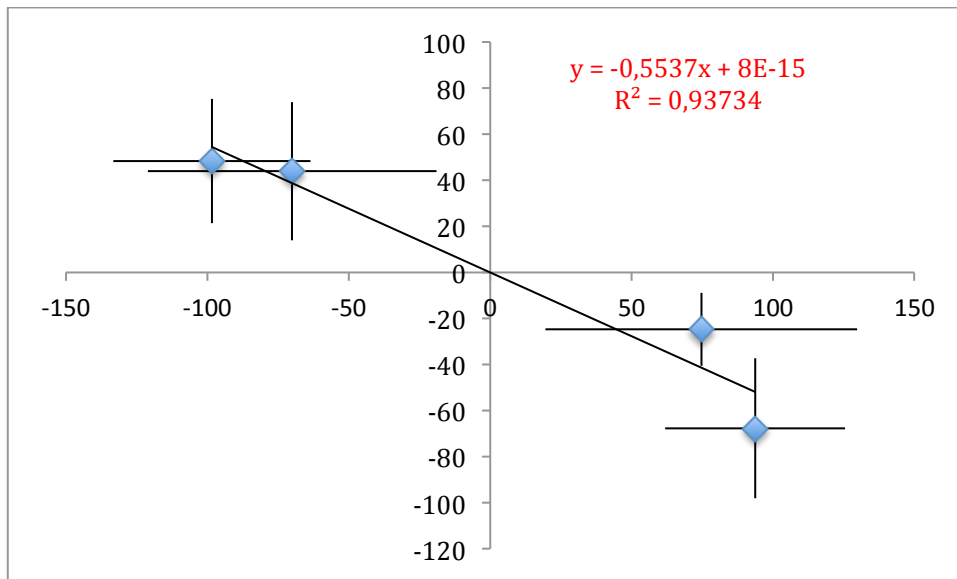


Fig. 3c Correlation between the difference in number of incursions and the difference in mortality during pairwise interactions, after the end of the experiment (mean± s.e.m.)

The fitted models showing the declining colony size over 42 days of the experiment, reveal demographic processes that vary among species combinations but also among replicates of the same species combination (Fig. 4).

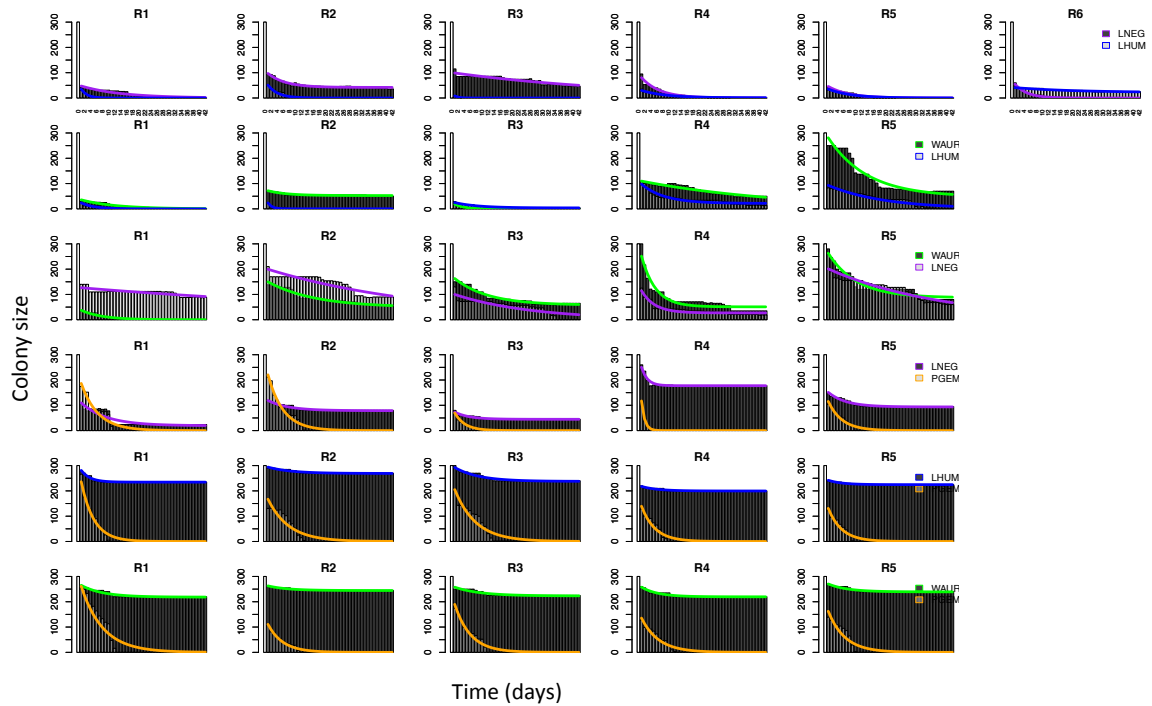


Fig. 4a Raw colony survival data (grey bars) and fitted model functions (colored lines) for all replicates of all pairwise species interactions. Each line represents replicates (R1-R6) of the same species interaction. LNEG = *L. neglectus*, LHUM = *L. humile*, WAUR = *W. auropunctata*, PMEG = *P. megacephala*.

When the estimated model parameters are represented in parameter space (Fig. 4b), different groups can be distinguished. All replicates of *P. megacephala* colonies (yellow discs, with the size of the disc representing the speed of mortality, parameter  $a$ ) have very high  $d$  values and  $p$  at values equalling 0, i.e. that species has a relatively high survival after the initial fights on the first day after connecting, but all colonies went extinct by the end of the 42-day observation. Similarly, almost all colonies of *L. humile* (blue discs) went extinct ( $p = 0$ ), except in the replicates where its opponent was *P. megacephala* (blue discs with yellow circles). This indicates *L. humile*'s dominance over *P. megacephala* but not over *W. auropunctata* and *L. neglectus*. In the interactions between *L. humile* and *L. neglectus*, both species suffer high initial mortality (low  $d$ ) and have a very low final colony size (low  $p$ ), but both parameters are slightly higher in *L. neglectus*. Additionally, the mortality parameters for *L. neglectus* faced with *P. megacephala* (purple discs with yellow circles) are much higher than those of *L. humile* against *P. megacephala*, also indicating that overall *L. neglectus* has a slight competitive advantage over *L. humile*. Overall, *W. auropunctata* (green discs) was the top dominant species with very high survival against *P. megacephala* (green discs, yellow circles) and relatively high  $d$  and  $p$  values against *L. humile* (green discs, blue circles) and *L. neglectus* (green discs, purple circles).

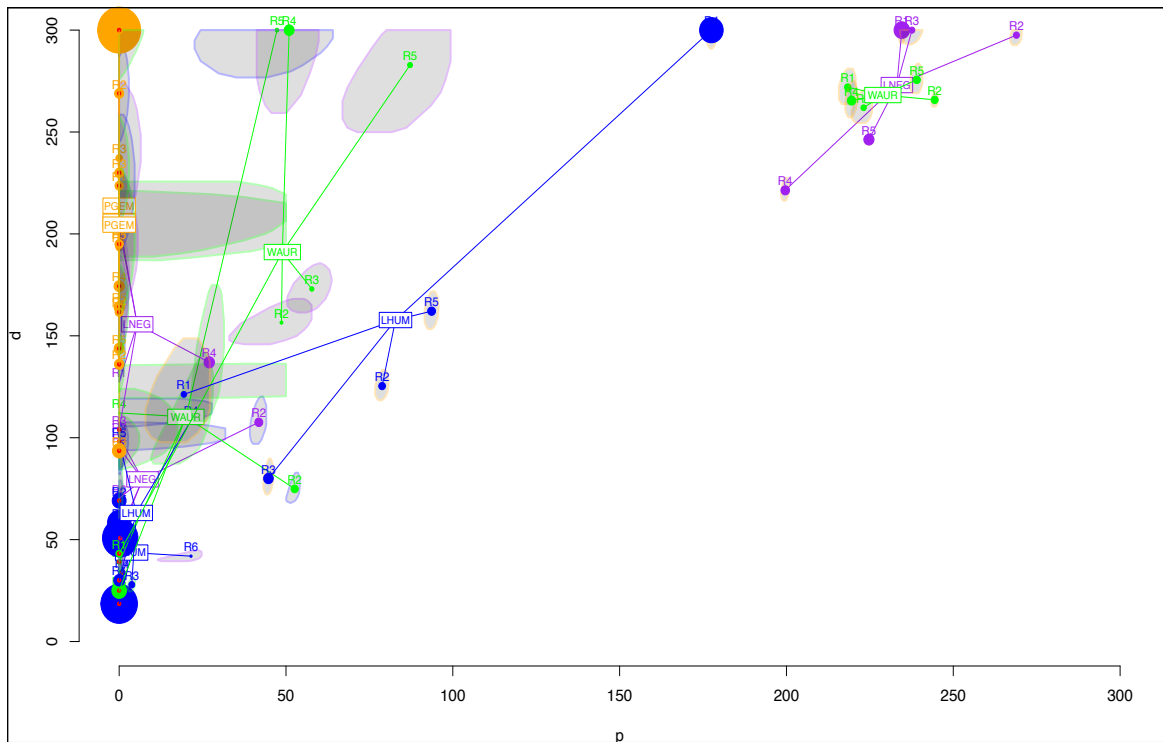


Fig. 4b Representation of the estimated model parameters,  $d$  is the initial survival after day 0,  $p$  is the final survival by the end of the experiment, the size of the coloured disc is proportional to parameter  $a$  (the slope, i.e. the speed and dynamics of mortality throughout the 42 days, the bigger the circle the faster the mortality), the colour of the bubbles indicates the species, the grey circle surrounding each bubble is the confidence envelope and the colour of the line surrounding the confidence envelope indicates the opponent species.

We then represented the estimations of mortality parameters on the 3 main axes of a Principal Component Analysis (Fig. 5a). The distances between points were then calculated and used to analyse clusters (Fig. 5b). These clusters show groups of colonies with similar survival processes. The clusters identified homogeneous groups, which do not necessarily correspond to all replicates of a given species, but rather to all replicates that follow a similar demographic process. Group 1 included colonies of *W. auropunctata* and *L. humile* with a homogeneous response to *P. megacephala*. Group 2 was a small group of three colonies with a particular behaviour, which are all replicates of different species interactions, illustrating that there was some individual variability among colonies of different replicates of the same species interaction. Group 3 contained almost exclusively *P. megacephala* faced with its three opponent species. Group 4 and group 5 showed the diversity of responses of the other three species, when faced with an opponent other than *P. megacephala*. *L. neglectus* was more associated with group 4 and *L. humile* with group 5. We then classified the data points representing individual models in the Principal Component space as members of one of the five groups (Fig. 5c). Because of the intra-group homogeneity, their behaviour can be expressed as a mean process (Fig. 5c).

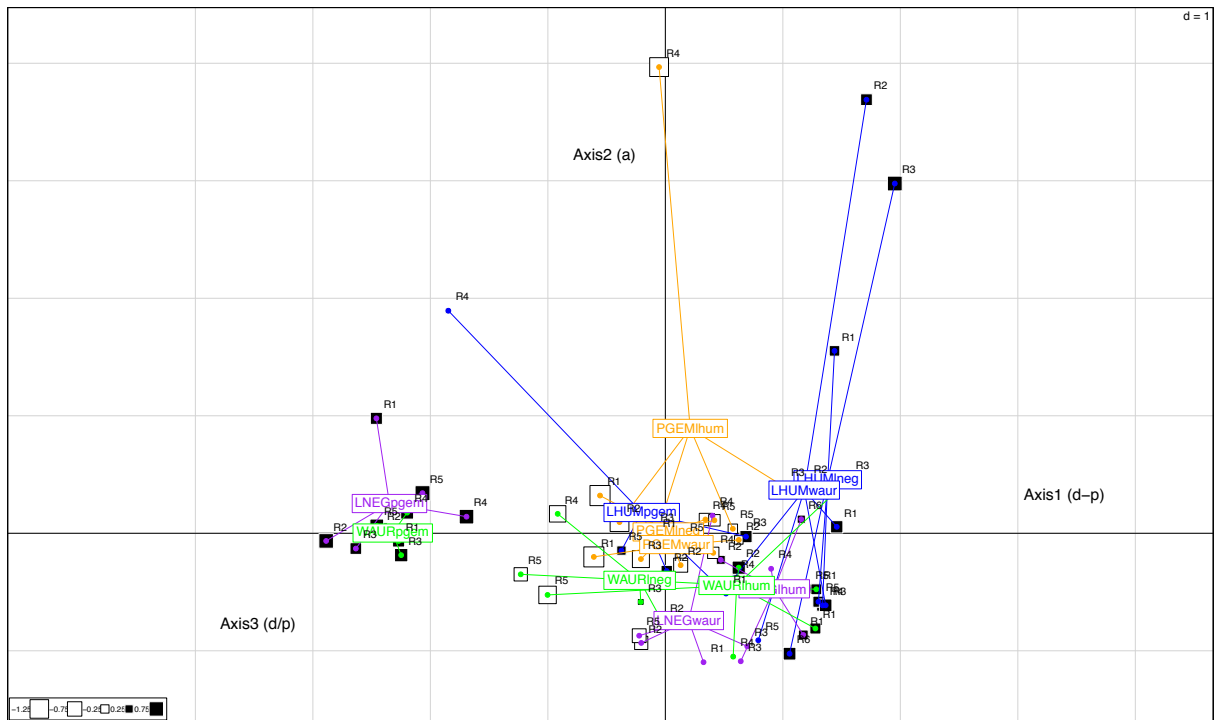


Fig. 5a Principal Component Analysis of the mortality parameters. The first axis is  $d-p$ , the second axis  $a$ . The third axis is  $d/p$  and is represented by squares: full squares indicates positive values, and empty squares negative values, the size of the square represents the distance to the axis1/axis2 plane). The species for which the model has been fitted is written in capitals, its opponent in lower case. Different colors represent the four species, along the same key than in other figures.

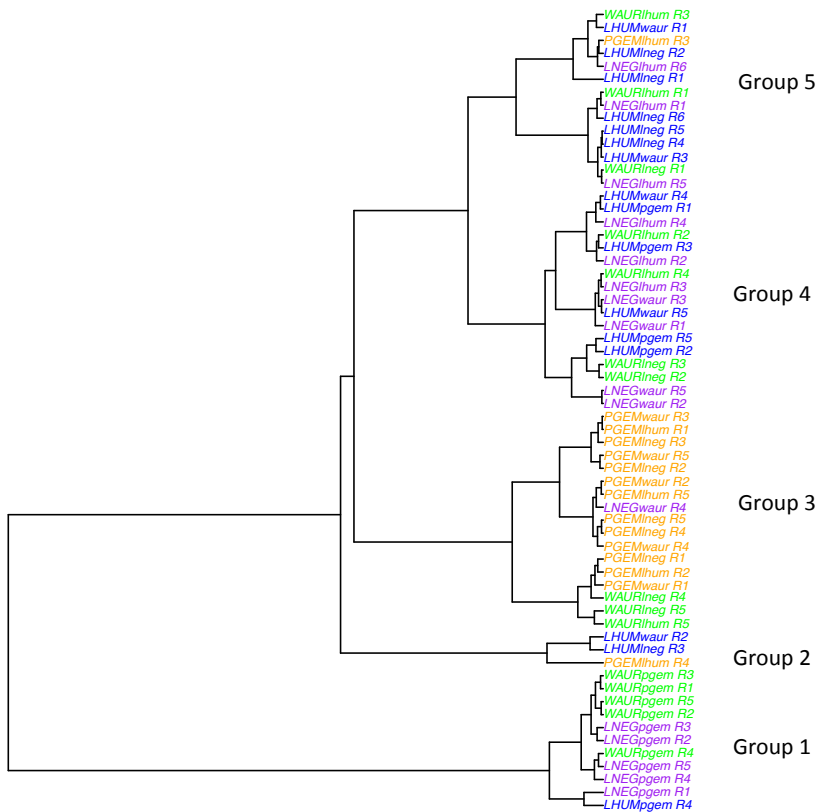




Fig. 5b Cluster analysis using the distance between models represented in the Principal Component Analysis. The cluster analysis identifies groups with similar survival processes. The species for which the model has been fitted is written in capitals, its opponent in lower case. R1-R6 indicate the identity of the replicate.

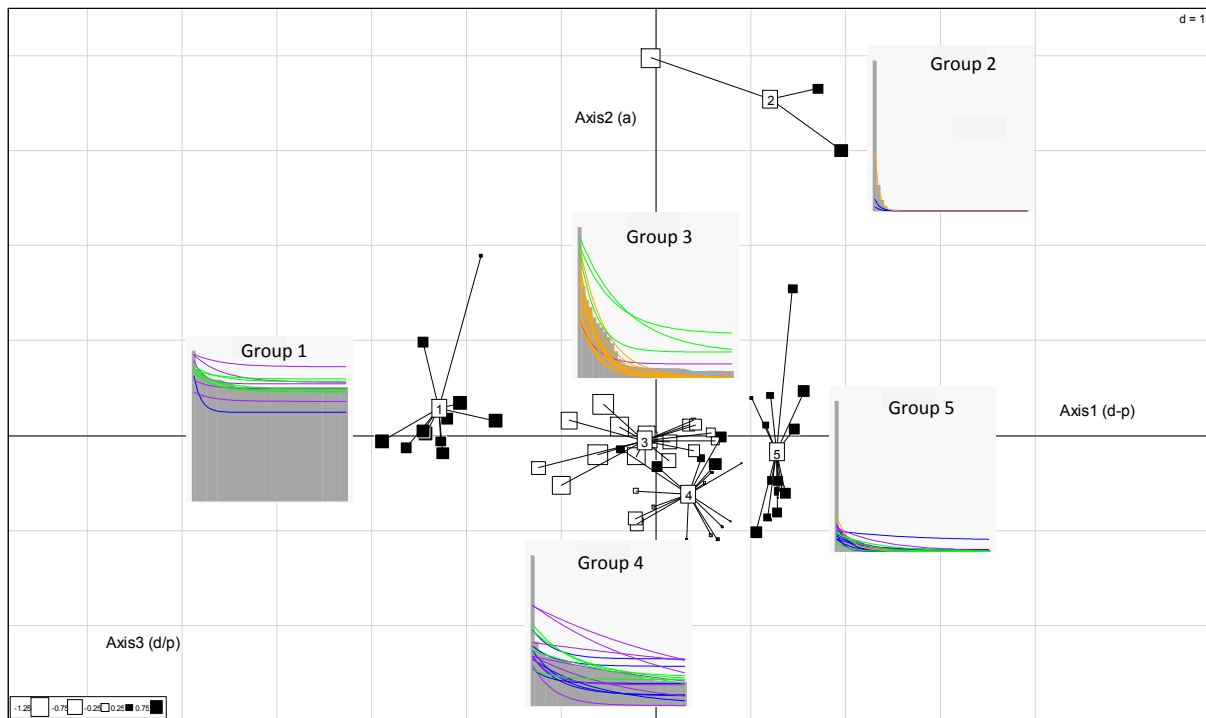
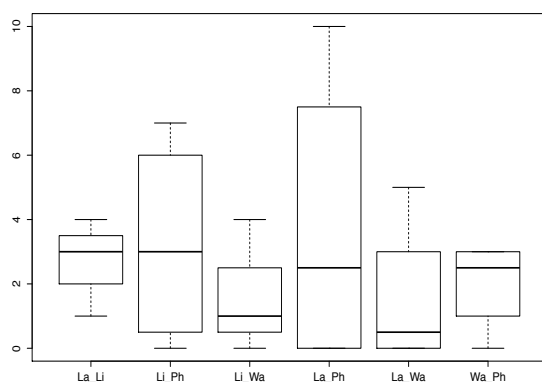


Fig 5c Five groups identified by the cluster analysis and their mean survival process (grey bars) and individual models included in each group (coloured lines). Each colour corresponds to a species (yellow = *P. megacephala*, green = *W. auropunctata*, blue = *L. humile*, purple = *L. neglectus*). The points represent the parameter combination for individual colonies.

### 3.2 Multi-colony interactions

During simultaneous interactions among colonies of all four species, all species participated equally in fights. No significant difference in the number of fights was observed among species pairs (Fig. 6a) ( $\chi^2_{(5)} = 1.7935$ ,  $p=0.8769$ ). Similarly, all species displayed nest blocking behaviour, and no significant differences among species were observed ( $\chi^2_{(3)} = 5.8802$ ,  $p=0.1176$ ) (Fig. 6b).



Kruskal-Wallis test  $p=0.8769$

Fig. 6a left: Number of pairwise fights during interactions of all four species simultaneously; right: proportion of pairwise fights

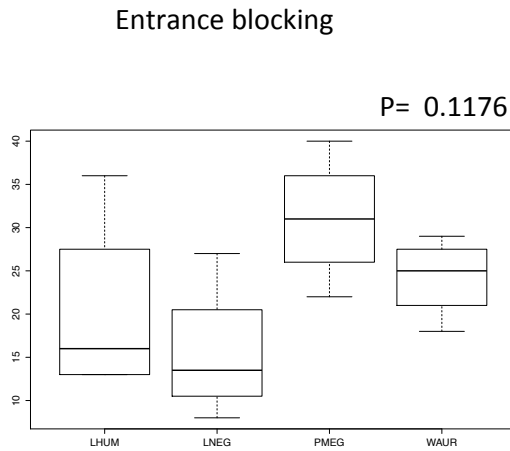


Fig. 6b Number of workers engaged in entrance blocking during 4 colonies interactions

In all 4 replicates, a single species survived after 2 weeks of interaction. The mortality was high in all cases and the surviving colony had a very reduced size. In replicate 1, *L. neglectus* survived with 20 workers and 1 queen; in replicate 2, *P. megacephala* survived with 7 workers and 2 queens; in replicate 3, *P. megacephala* survived with 17 workers and 2 queens and in replicate 4, *W. auropunctata* survived with 30 workers and 2 queens.

#### 4. DISCUSSION

Connecting adjacent foraging arenas of species pairs among four of the most invasive ant species, *W. auropunctata*, *L. neglectus*, *L. humile* and *P. megacephala* resulted immediately in aggressive interactions. After intense fighting over the first hours after colony connection, fragments of both colonies survived and declined in size over 42 days of observation. In these experiments, the least dominant species was *P. megacephala*, which always went extinct, although its initial mortality on the first day of interaction was comparatively low (Fig. 4). Interactions among the three remaining species showed more complex dynamics. In all three pairwise interactions, both opponents won the interaction in at least one replicate. As different replicates of the same interaction followed different dynamics, it would not be representative to simply average the survival data across replicates. Instead, models were fitted for each colony individually and then the estimated parameters were represented in a parameter space, allowing to analyse clusters of mortality dynamics. This captured more accurately the central tendency of each species interaction. Generally, *W. auropunctata* and *L. neglectus* were the most dominant species and *L. humile* tended towards extinction in all interactions except against *P. megacephala*. *L. neglectus* was slightly less competitive than *W. auropunctata*. Overall, this dominance hierarchy is consistent with the results found in classical petri-dish interference interactions between small groups of workers (Bertelsmeier in prep). However, our results demonstrated more complex dynamics, rendering the outcome of pairwise species interactions less predictable. In all replicates a steep decrease in colony size was followed by a slower decrease over several weeks. Connecting more than two interacting colonies, to mimic a multiple invasion scenario, adds another level of complexity. The outcome of the 4 colonies experiment was

extremely variable, with three different species winning in four replicates. Surprisingly, in two cases the last surviving species was *P. megacephala*, which always went extinct during pairwise interactions and was thus regarded as the weakest of the four species, here and in the petri dish experiment (Bertelsmeier in prep). These dynamics observed at the whole-colony level would not be possible to predict based on classical worker-worker interactions. To our knowledge, this is the first medium-term experiment with invasive ants recording the dynamics of colony interactions on a daily basis.

The four species varied strongly in their exploratory behaviour when the adjacent colonies were connected. In particular *P. megacephala* and *L. humile* invaded rapidly the arena of the opponent species, leading to a high proportion of fights occurring on the territory of the opponent. *W. auropunctata* and *L. neglectus*, on the other hand, were slower, more passive explorers. Interestingly, the species had the highest tendency to invade the opponent's territory suffered the highest mortality. This suggests a disadvantage for invasive ant species to exhibit strong exploratory behaviour for interference competition, at least faced with other invasive ant species that are better at interference competition. Probably these species encounter rarely other very aggressive and dominant species in the ant communities they invade.

In native ant communities, one factor promoting co-existence between species is a trade-off between the species' ability to discover and their ability to dominate resources<sup>9,14,15</sup>. However, it has been suggested that invasive ants break this discovery-dominance trade-off by excelling at discovering and dominating resources. This is thought to be an important mechanism leading to their high impacts on native communities by competitively displacing many species<sup>30</sup>. Future research may investigate whether there is such a trade-off among invasive ants and whether all of them generally break the trade-off relative to native species.

Although experiments at the whole colony level offer greater realism than behavioural observations over a few minutes in petri dishes, they still suffer from certain limitations. For example, the degree of resource dispersion and habitat complexity<sup>31</sup>, as well as habitat type or disturbance can modify dominance hierarchies<sup>9,32</sup>. In addition, the space where adjacent colonies could interact was constrained by the experimental set-up and it may be possible that colonies would not annihilate each other if they were spaced over a few meters, although this scenario is unlikely given that invasive ants can even have impacts on native species at a biogeographic scale<sup>33</sup>. Further, different climatic suitability of a certain area can favour one species over the other, giving a competitive advantage to one species over another (ex. Rice & Silverman, 2013). Such a dominance shift is especially likely in species pairs, which do not differ much in their capacity to dominate (e.g., *L. neglectus* and *L. humile*). Additionally, biotic interactions can alter dominance hierarchies, for example the presence of phorid flies can compromise the competitive abilities of some ant species but not others<sup>14</sup>. Field experiments could be useful to determine the relative dominance of entire colonies under a given set of environmental conditions, using secure, artificial nests for example to guarantee biosecurity (Luque et al. submitted, Chapter 11). Another interesting question is how different initial colony sizes would impact the outcome of colony-colony competition. Is there a certain ratio at which dominance would be inverted or a clear winner can be predicted in cases where the hierarchy was not clear-cut at equal group size? Further, the effect of a 'resident' colony versus an arriving colony might be investigated.

Overall, co-existence between highly aggressive invasive ant species seems unlikely, given the extremely high mortality immediately after connecting nests. These findings are consistent with the observation of mosaics of areas dominated by different invasive species in New Caledonia (Hervé Jourdan, pers. comm.). However, predicting the winner of a symmetrical colony-colony interaction is not as straightforward as predicting the winner of a worker-worker interaction (e.g. Blight et al., 2010; Buczkowski & Bennett, 2007; Kirschenbaum & Grace, 2008, Bertelsmeier et al. in prep.). This study shows the importance of scaling up to the colony level. It would be interesting to carry out complementary experiments in the field, using secure artificial nests with different invasive ant species to test their interaction under more realistic conditions (using the experimental device outlined in Chapter 11). In addition, this type of field experiments would allow to test the influence of different environmental conditions (e.g. temperature) on the behavioural interaction between invasive ants. This is particularly interesting in the context of on-going global changes.

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# Is there a discovery-dominance trade-off among invasive ants ?

Cleo Bertelsmeier, Amaury Avril, Olivier Blight, Hervé Jourdan and Franck Courchamp





# 14. Discovery-dominance trade-off

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## 1. INTRODUCTION

Worldwide, ant invasions are an enormous threat to biodiversity<sup>1-3</sup>. Mostly of tropical and subtropical origin, invasive ants have succeeded in colonizing every continent on Earth and very diverse types of habitats<sup>4</sup>. Frequently, many interconnected nests form large supercolonies that monopolize nesting space and food resources<sup>1</sup>. Native ants only rarely succeed in coexisting with invasive ants and are displaced or can even go locally extinct<sup>1-3</sup>. In invaded areas, the abundance of native ants can be reduced by over 90%<sup>5</sup>. Evidence for the impact of invasive ants comes largely from correlational studies (<sup>1,3</sup> and refs therein), demonstrating exclusive distributions of native and invasive ants<sup>6-8</sup>; the displacement of native ants at invasion fronts<sup>6-8</sup> and large scale patterns in ant co-occurrence and diversity<sup>9</sup>. Lab or field based studies have revealed differences between native and invasive ants in diet, aggressiveness, thermal preferences and periods of activity<sup>1</sup>. However, rarely the causal link between a certain difference in traits and the displacement of native ant species has been tested. Nonetheless, numerous hypotheses exist to explain the emergence of the ‘invasive syndrome’<sup>10</sup>. High levels of aggressiveness and high interference abilities may allow defending and monopolizing resources<sup>1</sup>. In addition, preference for sugary substances can lead to a diet higher in carbohydrates, which has been linked to higher colony growth rates and increased aggressiveness<sup>11</sup>. Probably different factors play a role in the invasion process and could work in concert. Whichever the predominant factor, all potential explanations of invasiveness are directly or indirectly related to an enhanced capacity to either dominate resources or to discover and exploit them. Native ant communities are strongly structured by competition<sup>12-15</sup>, and the interaction between traits promoting interference or exploitative competition can promote coexistence<sup>16</sup>. There is a well studied trade-off between the capacity to discover resources and the capacity to defend them<sup>15,17-19</sup>. We hypothesize that invasive ants may not simply excel at one or the other, but at both. The Argentine ant, *Linepithema humile*, has been shown to break this discovery-dominance trade-off in a native ant community in the Southern United States<sup>20</sup>, *i.e.* the species is both better at discovering and dominating the resources than the native ant species. The violation of this discovery-dominance trade-off<sup>15,17-19</sup>, can lead to clear advantage over the species excelling in one characteristic at the systematic loss of the other. This competitive advantage over local ant species can lead to the near complete loss of ant diversity and provides a direct mechanism of invasiveness<sup>6</sup>. However, it is unknown if other invasive ants excel at both interference and exploitative competition or whether this conclusion is only valid for *L. humile*. Given, the high number of invasive ants (19 listed by the IUCN<sup>21</sup>) and their high impacts on biodiversity, agriculture, health and economy<sup>1-3</sup>, it is urgent to get a better understanding of the mechanisms of invasiveness.

The objective of our study is to test (1) whether four of the worst invasive ants differ in their exploration and exploitation behaviour, *i.e.* their ability to discover resources and successfully recruit nestmates, (2) whether differences are related to their capacity to dominate in interference competition.

As a model system, we use four highly invasive ants, which have been previously shown to form a linear dominance hierarchy in interference competition (Bertelsmeier et al, in prep. Chapter 12): *Wasmannia auropunctata* > *Lasius neglectus* > *Linepithema humile* > *Pheidole megacephala*. Knowing if these species form the same hierarchy in exploitative competition will allow testing our hypothesis that all four highly aggressive species also excel in exploitation competition, which allow them to break the discovery-dominance trade-off, and thereby gain competitive advantage over species in invaded ant communities. If the most invasive ants species all break the discovery-dominance trade-off, this would represent a clear mechanism of invasion.

Here, we use two experiments to test the species' capacities to discover and exploit resources. The first is an exploitation experiment, where food resources were placed directly in front of the nest to test which species is the fastest exploiter. The second experiment tests the species' abilities to explore quickly their environment by separating the nest from a food source by a maze.

## 2. MATERIAL AND METHODS

### *Colony collection and maintenance of laboratory colonies*

The ants were collected between March and December 2012 in New Caledonia (*W. auropunctata* and *P. megacephala*) and in Southern France (*L. humile* and *L. neglectus*). Colony fragments were maintained in large plastic nest containers (55x 35x 25 cm) filled with substrate from the original nesting site (soil, wood, leaves) and contained several tubes of water. These boxes were kept at  $24 \pm 2^\circ\text{C}$  with the appropriate soil moisture. The ants were fed daily with a variant of the Bhatkar diet <sup>22</sup>.

### *Exploitation experiment*

Prior to the experiment, the ants were starved for one week. Subsequently, a colony of 300 workers and one queen was collected and placed into a small plastic nest (11 x 8 x 4.5 cm), filled with plaster at an appropriate humidity and covered with a red filter. The entrance of the nest was a small plastic tube (diameter 0.8 cm, length 3 cm), touching the foraging arena (Fig. 1a). The entrance of the nest was blocked with a piece of cotton and the ants were allowed to acclimatize for 24h, before the cotton was removed. Three baits (tuna, sugary water and a seed mixture) were placed on aluminium foil at a distance of approximately 6 cm from the nest entrance, at a random order. We recorded foraging behaviour for two hours with a camera taking a picture every ten seconds (i.e., 720 photos per trial). We recorded the time until discovery of the baits (arrival of the first ant), time until recruitment (defined as five workers present simultaneously at a bait), the maximum number of workers observed simultaneously at a bait and the total number of workers observed at a bait. After each experiment, the foraging arena was cleaned and pheromone traces were eliminated with alcohol. Each colony was only used in one single trial. We carried out ten replicates per species.

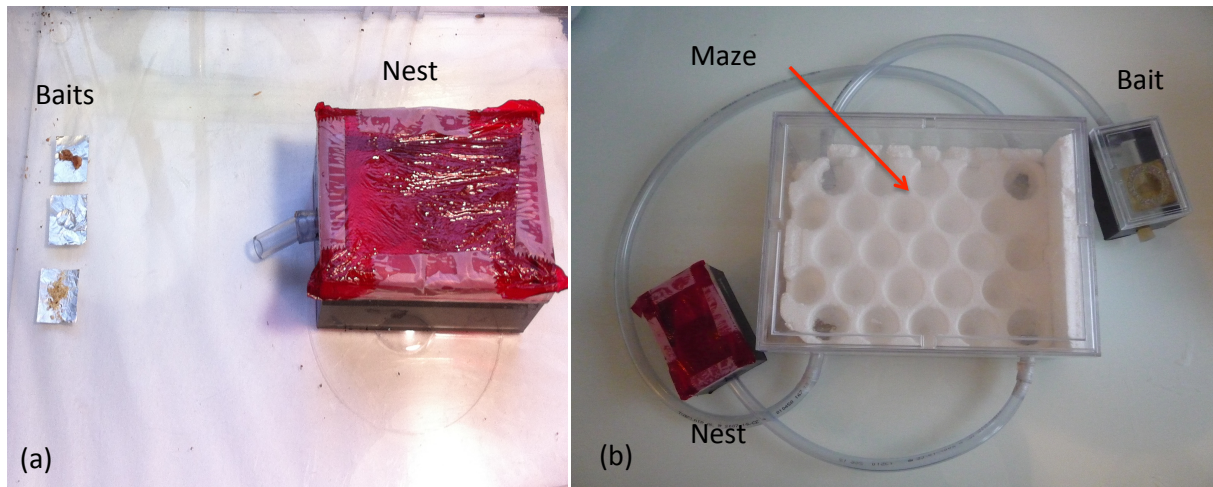


Fig. 1 a) Set-up of the experiment testing exploitative abilities, b) set-up of the maze testing explorative abilities.

### Exploration experiment

Prior to the experiment, the ants were starved for one week. Subsequently, a colony of 300 workers and one queen was aspirated and placed into a small plastic nest (11 x 8 x 4.5 cm), filled with plaster at an appropriate humidity and covered with a red filter. The entrance of the nest was connected through a long plastic tube (diameter 0.8 cm, length 40 cm) to an exploration arena (24 x 17.5 x 10 cm) (Fig 1b). The exploration arena contained a polystyrene structure (25 holes 3 cm deep, with a diameter of 2.8 cm), which constituted a 3D 'maze' that the ants needed to explore in order to find the foraging arena. At the diagonal opposite to the nest, another plastic tube (diameter 0.8 cm, length 40 cm) was connected to a small foraging arena (11 x 8 x 4.5 cm), where a bait (honeyed water) was placed. The bait was chosen because of its universal attractiveness to all of the four invasive ant species. The two other diagonals of the exploration arena were connected to each other through a longer plastic tube (diameter 0.8 cm, length 60 cm). The entrance of the nest was blocked with a piece of cotton and the ants were allowed to acclimatize for 24h, before the cotton was removed and the exploration arena was accessible. We recorded foraging behaviour in the small foraging arena for 40 hours with a camera taking a picture every two minutes (in total 1200 photos per trial). We recorded the time until discovery of the baits (arrival of the first ant), time until recruitment (defined as five workers present simultaneously at a bait) and the maximum number of workers. It was not possible to record the total number of workers that have visited the bait in this experiment because of the time lapse of two minutes between pictures, which does not allow to track individuals. After each experiment, the whole set-up was cleaned and eventual pheromone traces were eliminated with alcohol. Each colony was only used in one single trial. We carried out five replicates per species.

In both experiments, colonies of *P. megacephala* contained 10% of major workers.

### *Interference competition*

To test the relationship between discovery/ exploitation and behavioural dominance, we used data from a previous study on interference competition among invasive ants (Bertelsmeier, in prep). The study used classical dyadic confrontation experiments in petri dishes, using single worker and group (10 workers) interactions. Based on the confrontations of each species with each of six other invasive ants, a 'survival' index (SI) was calculated for each species, reflecting its capacity to survive all pairwise interactions (Chapter 12). In addition, a 'killing' index (KI) was calculated, reflecting the species' capacity to kill its opponents in pairwise interactions (Chapter 12). As, both SI and KI were based on pairwise interactions of seven species we recalculated both indices for only the four species in our study. This was achieved by taking into account only the scores of each species achieved when confronted with the three other species used in our study.

### *Analyses*

Prior to statistical analysis of the differences in SI and KI among species, we examined all data distributions using the Shapiro Wilk W test for normality. Because data did not conform to a normal distribution, we used the nonparametric Kruskal-Wallis rank sum test, adjusting for multiple comparisons with a Kruskal multiple comparison test of the `kruskalmc()` function included in the `girmess` package in R.

In cases where 'discovery' or 'recruitment' was not observed over the duration of the experiment, the maximum time was assigned to the colony. As we used rank-based nonparametric tests, this attributes the last discovery rank to all colonies (which are considered *ex aequo*) that did not discover the resource in the given time (or failed to recruit to it). This means that we did not need to run the experiments until the slowest species found the baits or recruited over it.

Subsequently, we test if the species' capacity to discover resources and/or recruit to them are correlated to their behavioural dominance score. As both dominance indices, SI and KI, are very tightly correlated ( $r^2=0.9738$ ), we only used one, SI, behavioural dominance score. The discovery/recruitment variables are measured in time, and therefore higher values indicate slower, less competitive species. For the sake of presentation and interpretation, we preferred here to present these variables so that a higher score would equal a higher ability, in order to be able to compare with dominance scores (which are higher for more dominant species). We therefore transformed the variables into a Discovery or recruitment score (total time of the experiment – time until event (discovery or recruitment)). In case of a very fast discovery, the score approaches the maximum time of the experiment, and when the event did not occur, the score equals 0.

## **3. RESULTS**

The four species form a linear dominance hierarchy, with SI and KI being tightly correlated (Fig. 2).

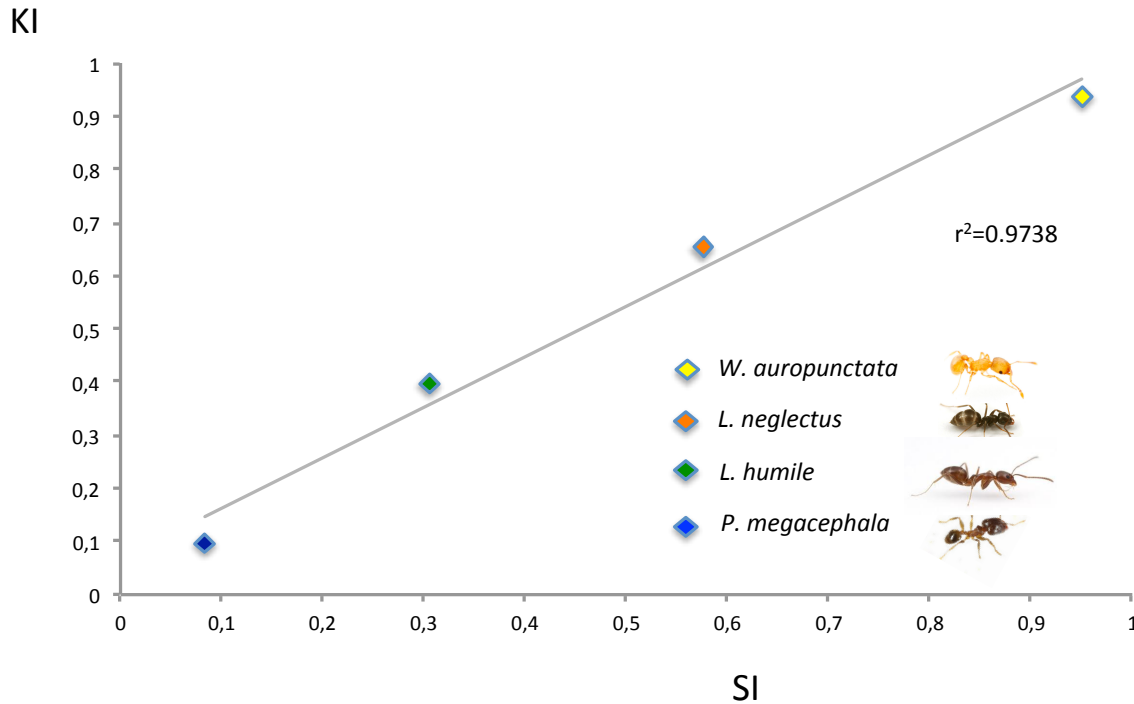


Fig. 2. Dominance hierarchy in interference competition. SI = Survival index, KI = killing index

In the exploitation experiment, the highest number of workers was observed at the sugar bait across all four species (Fig. 3). The differences in diet preferences were significant for all species, except *W. auropunctata* (Kruskal Wallis test: *L. humile*  $\chi^2_{(2)} = 25.8525$ ,  $p < 0.0001$ , *L. neglectus*  $\chi^2_{(2)} = 18.0008$ ,  $p = 0.0001234$ , *P. megacephala*  $\chi^2_{(2)} = 23.3969$ ,  $p < 0.0001$ , *W. auropunctata*  $\chi^2_{(2)} = 5.1038$ ,  $p = 0.07793$ ). Pairwise comparisons among baits revealed a further preference of *L. humile* for tuna over seeds (Fig. 3), but in the two remaining species, *L. neglectus* and *P. megacephala*, the difference between tuna and seeds was not significant. Given that all four species were mostly attracted by sucrose and always discovered it first, in the following section 'time to discovery' is always the time until the first worker arrived on the sucrose bait. The cumulative number of workers at baits is the total number of ants that visited baits (all three baits pooled).

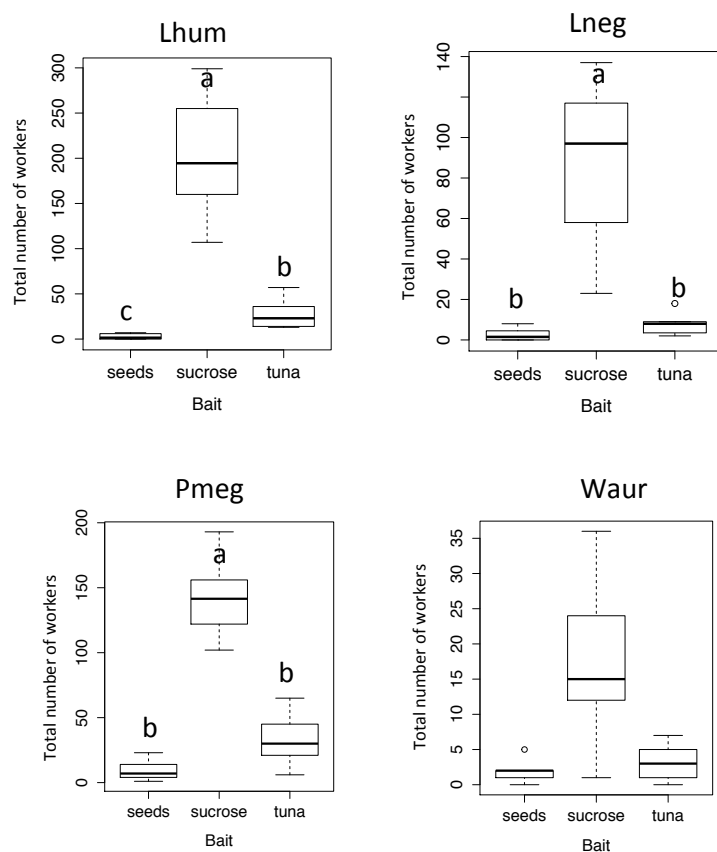


Fig. 3 Cumulated number of workers observed during 2h at each of three baits, averaged over the ten replicates  $\pm$ sd. Lhum = *L. humile*, Lneg = *L. neglectus*, Pmeg = *P. megacephala*, Waur = *W. auropunctata*

#### Exploitation experiment

Species differed significantly in discovery time ( $\chi^2_{(3)} = 22.3474$ ,  $p < 0.0001$ ) and recruitment time ( $\chi^2_{(3)} = 30.188$ ,  $p < 0.0001$ ), in both cases *L. humile* and *P. megacephala* were again the fastest, followed by *L. neglectus* and *W. auropunctata* (Fig. 4a). Further, species differed significantly in the maximum number of workers observed simultaneously at baits (Kruskal test  $\chi^2_{(3)} = 30.694$ ,  $p < 0.0001$ ), with *P. megacephala* and *L. humile* recruiting the highest number of workers (Fig. 4a). In addition, species differed significantly in the total, cumulated number of workers that visited baits over the 2h of the experiment ( $\chi^2_{(3)} = 30.188$ ,  $p < 0.0001$ ), with again *P. megacephala* and *L. humile* recruiting the highest number of workers (Fig. 4a).

## Baiting (exploitation)

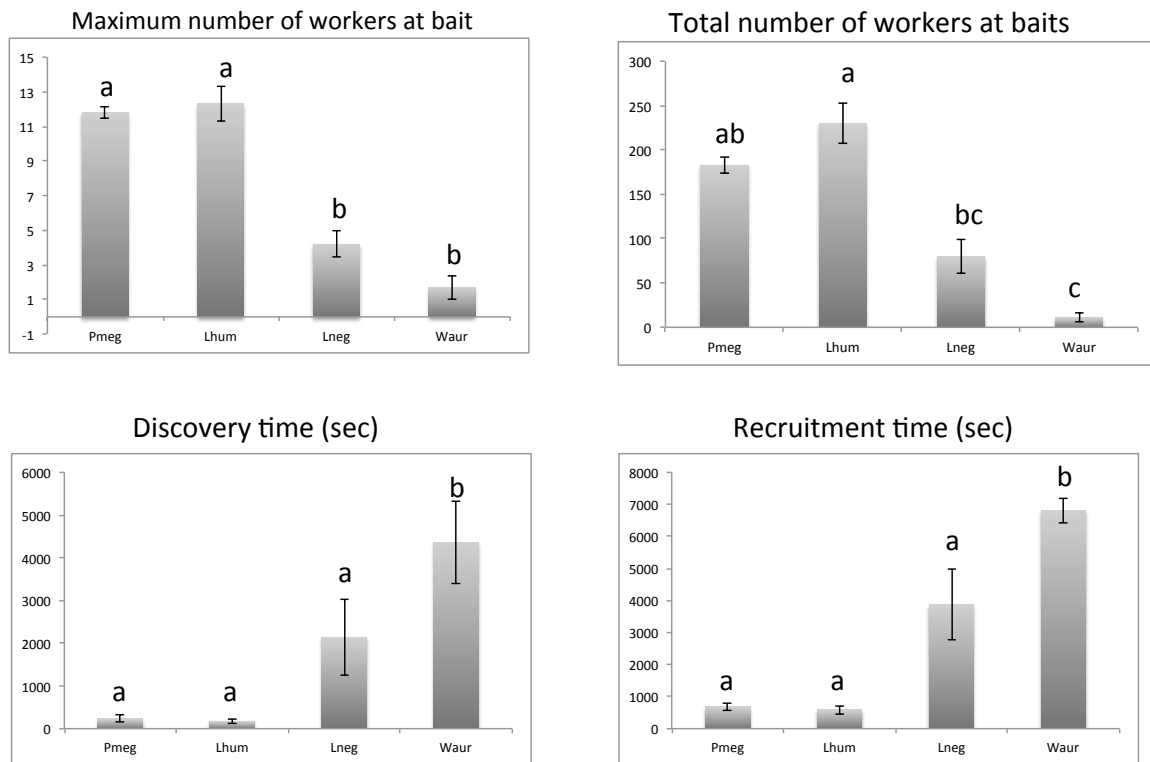


Fig. 4. Differences among species in a) the maximum number of workers observed simultaneously on baits, b) the total, cumulated number of workers visiting baits over 2h, c) time until discovery of the bait, c) time until recruitment with 5 workers simultaneously at a bait. Different letters denote significant pairwise comparisons in the post-hoc multiple comparison Kruskal-Wallis test. Values are given  $\pm$  s.e.m.

### Exploration experiment

Species differed significantly in discovery time ( $\chi^2_{(3)} = 14.8191$ ,  $p=0.001978$ ) and recruitment time ( $\chi^2_{(3)} = 14.6721$ ,  $p=0.002119$ ), in both cases *L. humile* and *P. megacephala* were again the two fastest, followed by *L. neglectus* and *W. auropunctata* together (Fig. 4b). Further, species differed significantly in the maximum number of workers observed simultaneously at baits (Kruskal test  $\chi^2_{(3)} = 13.5312$ ,  $p=0.003618$ ), with here again *P. megacephala* and *L. humile* recruiting the highest number of workers simultaneously over the 40h of observation (Fig. 4b).



## Exploration (maze)

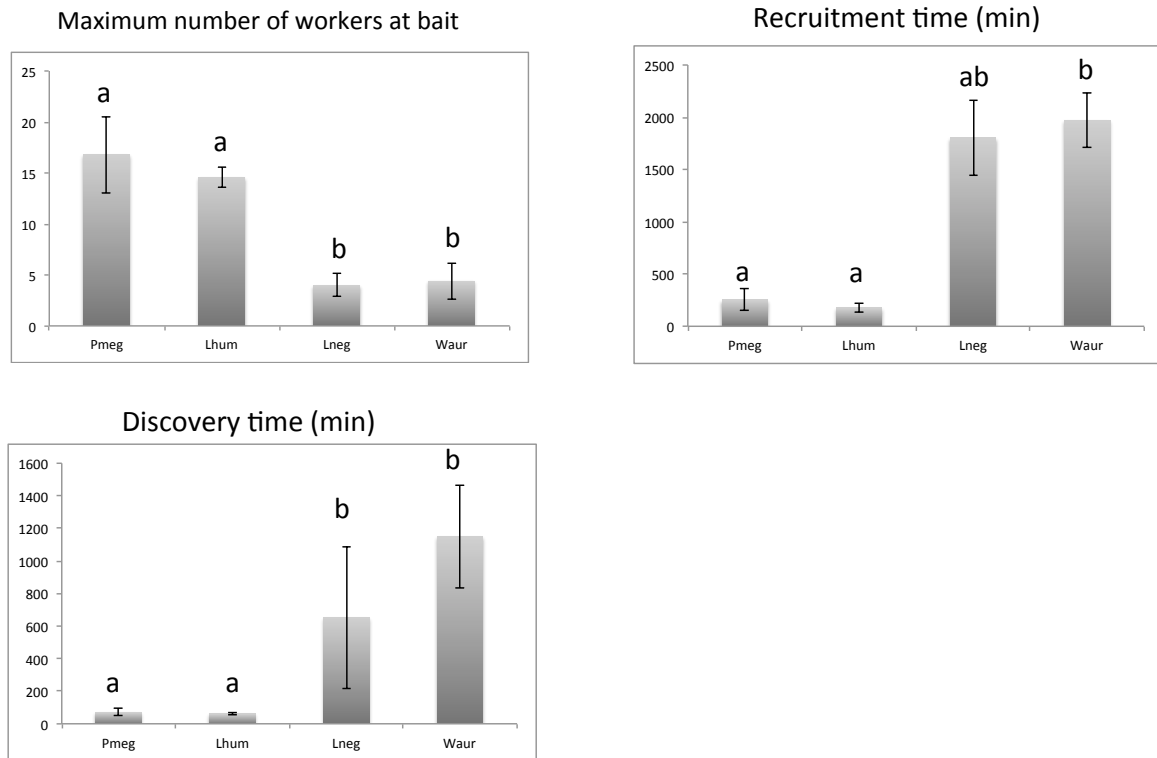


Fig. 4b Differences among species in a) the maximum number of workers visiting simultaneously baits, b) time until discovery of the bait, c) time until recruitment with 5 workers simultaneously at a bait. Different letters denote significant pairwise comparisons in the post-hoc multiple comparison Kruskal-Wallis test. Values are given  $\pm$  s.e.m.

### Discovery-dominance trade-off

In the exploitation experiment, discovery and exploitation abilities were negatively related to dominance (Fig. 5). The most dominant species had a lower discovery ( $r^2=0.927$ ,  $p=0.0331$ ) and recruitment speed ( $r^2=0.922$ ,  $p=0.03315$ ). They also recruited a lower maximum number of workers simultaneously ( $r^2=0.801$ ,  $p=0.061$ ) and a lower total number of workers ( $r^2=0.6977$ ,  $p=0.1064$ ).

The same pattern was observed in the 40h exploration experiment, where discovery and exploitation abilities were negatively related to dominance (Fig. 5). The most dominant species had a lower discovery ( $r^2=0.9045$ ,  $p=0.03235$ ) and recruitment speed ( $r^2=0.7084$ ,  $p=0.1025$ ) and recruited a lower number of workers simultaneously ( $r^2=0.6975$ ,  $p=0.165$ ).

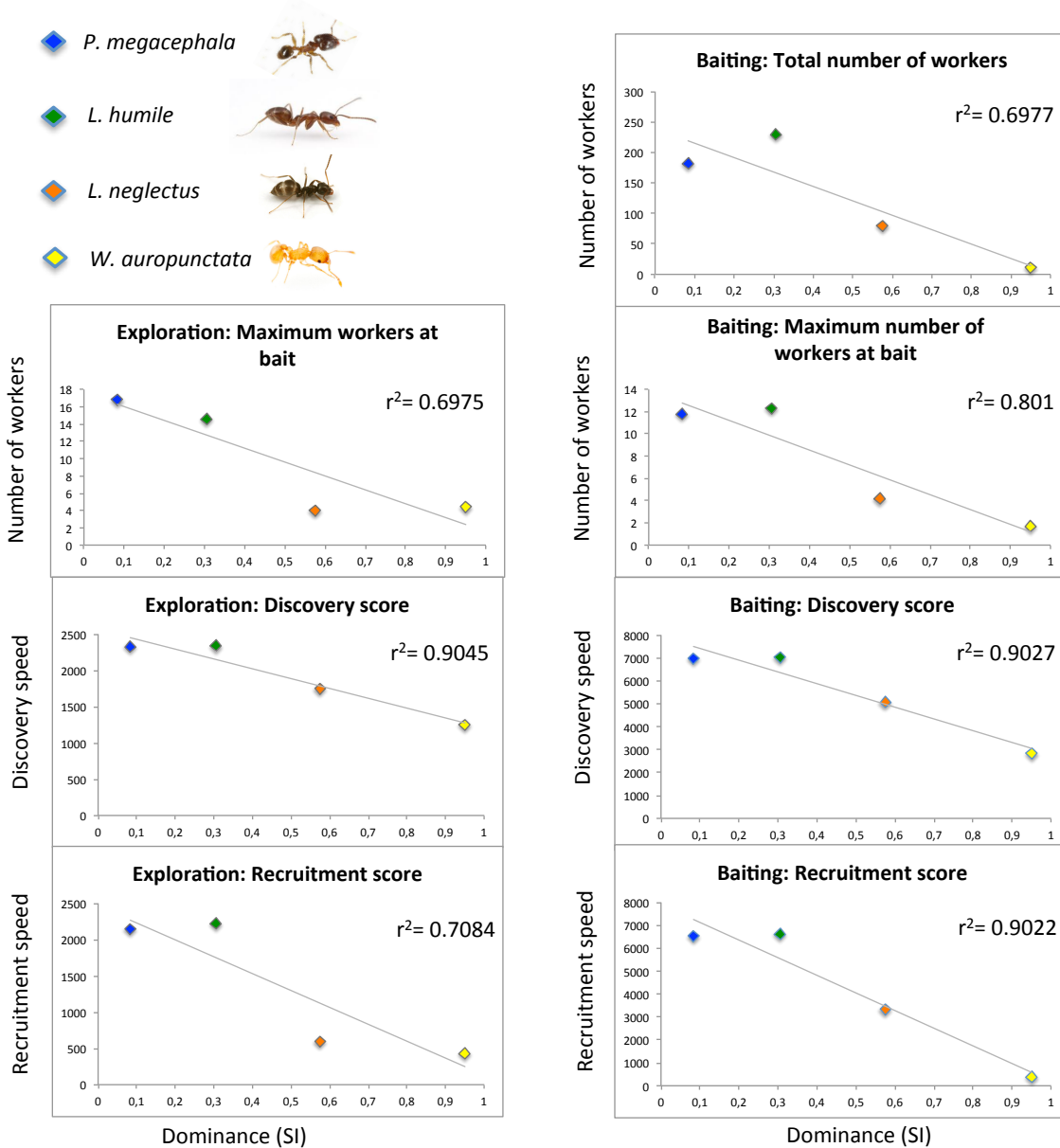


Fig. 5

#### 4. DISCUSSION

##### Main findings

The exploitation experiment and the exploration experiment showed that the capacity to discover resources and the capacity to exploit them by quickly recruiting a high number of nestmates to a resource are correlated in invasive ants. Combining these results with the hierarchy based on interference competition, we were able to show a negative relationship between both exploitation and exploration on the one hand and the capacity to dominate behaviourally on the other hand. This supported the idea of a negative dominance-discovery relationship among four of the worst invasive ant species. Consistently, *W. auropunctata*, has been shown to be the most dominant species in

dyadic confrontation experiments (Bertelsmeier in prep), surviving almost all interactions and killing most opponents. In the present study, this species was by far the slowest exploring and the least recruiting species. On the other hand *P. megacephala* and *L. humile*, which had very low dominance scores in dyadic confrontations, excelled at exploration and discovery abilities.

Our results thus suggest that, even though invasive ants may break dominance-discovery trade-offs in native communities<sup>20</sup>, there is a dominance-discovery trade-off among invasive ants. In uninvaded communities, the existence of a dominance-discovery trade-off is thought to promote species coexistence<sup>16</sup>, in spite of otherwise similar ecological niches. Therefore, the results of our study may be interpreted as a possibility of co-existence among the four highly invasive ants, studied here. Recent studies have suggested that these four invasive species could find suitable climatic conditions in the same regions of the world, arguing for potential interactions between them in multiply-invaded zones (Chapter 8 & 9). However, the current distribution of highly invasive ants seems exclusive so far, at least at a local scale<sup>23-25</sup>. A possibility is that no ultimate 'top invasive' ant species exists. Different species could excel at different capacities related to exploitation or interference. Local patches may be dominated by one species or the other, depending on environmental factors not considered in our study. This is consistent with the observation that *P. megacephala* and *W. auropunctata* form a mutually exclusive distribution in New Caledonia, each dominating different areas (Hervé Jourdan, pers. comm.). This pattern would not be predicted by the behavioural dominance hierarchy alone (Chapter 12), where *W. auropunctata* is the top dominant species and should exclude the three other species, forming a linear dominance hierarchy, in the absence of mitigating factors.

#### Limitations

One limitation of our study is that we compared the two sets of traits (interference vs exploitation) only among invasive species. Although these invasive species demonstrate a clear trade-off among them, it is conceivable that they all break that trade-off relative to native ants by being above average in their ability for both sets of traits. A way to resolve this issue would be ideally to compare interference and exploitation abilities of all four species to the native species of their respective invaded communities.

Our results on the dominance-discovery trade-off among invasive ants are, however, based on interactions among only four species and it would be interesting to consider a potential trade-off among a greater group of invasive ants to investigate the generality of this pattern. In addition, several limitations are inherent to the lab-based experimental approach used here. For example, the dominance-discovery trade-off might depend on habitat complexity. In an ant community of the Pacific atoll of Tokelau, it has been shown that *Anoplolepis gracilipes* was the first species to find and dominate food resources in low rugosity environments, but not in more complex environments<sup>26</sup>. In addition, source size and distribution matter. Small, dispersed resources favour quick discovery and removal times because smaller resources are more likely to be depleted by the discoverer, potentially resulting in a positive discovery-dominance relationship, rather than a trade-off<sup>27</sup>. On the other hand, large and clumped resources favour recruitment over a longer harvesting period. Aggressive behaviours are more likely to be successful at larger resources that can be defended<sup>27-29</sup>. A further limitation is that the baits are necessarily an artificial selection of different general types of resources (sugar, proteins, seeds). Although all ant species included in our study preferred sugary

substances, it remains possible different sugary resources could attract differently the four ant species. Another limitation are the laboratory conditions, which provide a neutral set-up without potentially mitigating biotic interactions, such as competitors or parasites that are known to influence the dominance-discovery trade-off<sup>18,30</sup>. Similarly, differences in temperature preferences are known to alter dominance relationships<sup>31-33</sup>. Another possibility is that the observed dominance-discovery trade-off is contingent on a certain colony size. Invasive ants generally reach very large colony sizes, often forming supercolonies<sup>1</sup>. Large colonies are more likely to discover resources by chance<sup>27</sup> and perhaps a large colony size can compensate for inherently poor exploration abilities, leading to an apparent violation of the dominance-discovery trade-off. In that case, the violation of the trade-off observed in the field would be a consequence of invasiveness, not the cause. At large colony sizes, it is possible that the trade-off is not only violated when invasive ants interact with native ant communities, but also when they interact with other invasive ant species. However, all four invasive ant species are capable of forming supercolonies, therefore the species can be compared because this advantage would not persist in comparison with the other invasive species.

#### *Implications*

Generally invasive ants are perceived as a homogenous group, sharing the same ecological traits and their aggressive behaviour is often invoked when explaining the displacement of native species. Frequently, invasive ants are compared to native ants but rarely among each other. It is generally assumed that invasive ants have the same 'invasive syndrome'<sup>1,10</sup>. However, this study shows that they do not only differ in the abilities at interference competition but also in their abilities at exploitative competition. Although it has become accepted that one possible mechanism explaining invasiveness is the violation of the discovery-dominance trade-off<sup>27</sup>, it is quite unexpected to find this trade-off among invasive ants.

An interesting question is whether invasive ants generally violate the trade-off in the invaded habitat or whether the mechanism of invasiveness differs among species, some excelling at exploitation/discovery, others at interference competition and others again at both. So far, it has been suggested that *Anoplolepis gracilipes* may break the trade-off in certain types of habitat<sup>26</sup> and similarly *Solenopsis invicta* has been shown to break the trade-off sometimes, but not always<sup>34</sup>. Although interference and exploitative competitions have been recognized as the two pillars of community ecology<sup>15</sup>, few studies have investigated exploitation and exploration, because interference is much easier to detect and interference competition between two species is a somewhat more direct interaction<sup>27</sup>.

To conclude, our results have shown a surprising dominance-discovery trade-off among four highly invasive ants. This opens new research question regarding the mechanisms of invasiveness in ants. In particular, it shows that invasive ants are not as a homogeneous group as generally assumed<sup>1,2</sup> and that they may employ different strategies to become invasive, some relying more on their interference superiority, some other on exploitation ascendancy. In addition, the interaction of different invasive ant species deserves further attention, especially in the light of on-going global change and increasing species introductions<sup>35</sup>. It is likely that areas suitable to several invasive ants will suffer from multiple invasions in the future and it is crucial to further improve the understanding of interactions among different invasive species.

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# Ant Profiler – a database of ecological characteristics of ants (Hymenoptera: Formicidae)

Cleo Bertelsmeier, Gloria M. Luque, Amandine Confais and Franck Courchamp





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## Forum

### Ant Profiler – a database of ecological characteristics of ants (Hymenoptera: Formicidae)

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**Abstract:** We developed a database of 24 major ecological characteristics of ants – "Ant Profiler" – which includes information on species morphology, colony dynamics, behaviour, habitat, nesting sites, diet, species interactions and distribution. Our database is a publically available research tool to study the ecology of ants and relies on the contribution of the myrmecologist community to provide information on ants. The specificity of our database, compared to other existing ant databases, is that it presents ecological information in a structured and standardized way instead of a descriptive text. The interface of our webpage makes information searchable and allows users to retrieve a list of species corresponding to any particular trait or combination of traits. The database allows downloading data that can be used by any statistic software for further analysis.

#### Introduction

Over the last decades, there has been an increasing awareness of the importance of ants for the understanding of ecology and ecosystem functioning. Ants do not only represent an important part of animal biomass (WILSON & HÖLDOBLER 2005) they also play important roles in numerous ecosystem functions – from seed dispersal to nutrient cycling in the soil (FOLGARAIT 1998, LACH & HOOPER-BUI 2010). The high diversity of ants in terms of number of species, ecological roles, reproductive systems, social organizations and life styles makes ants an ideal model system. Understanding the role of ants in ecosystems and factors that influence ant diversity and abundance is crucial for a wide range of scientists, especially ecologists and conservation biologists.

First, it would be interesting to simply have an estimation of the proportion of known species that present certain traits such as polygyny, or the proportion of species that are parasitic, slave-making or nest raiding. Such information, although basic and crucial, is currently lacking, despite many specialists being knowledgeable about many traits for subsets of species.

Second, many outstanding questions in ecology and evolution concern the analysis of global patterns and correlations of species' traits. For example, recent studies have attempted to find correlates of geographic distributions of ants (GERAGHTY & al. 2007), to relate the species' ecology to phylogeny (JANDA & al. 2004, MACHAC & al. 2011), to investigate traits of invasive species (MCGLYNN 1999, LESTER 2005, WITTENBORN & JESCHKE 2011), or to test correlates of stress-tolerance (DIAMOND & al. 2011). How-

ever, these correlative studies have generally used a small subset of species (e.g., North American ants). A global database of ecological characteristics would allow further and more robust investigation of these questions and it would allow asking many more. For example, it would be interesting to search for traits associated with polygyny or different modes of colony foundation (NAKAMARU & al. 2007). It would be possible to investigate factors related to different colony sizes (HOLBROOK & al. 2011), reproductive strategies (BOOMSMA & al. 2009), different foraging behaviours (MOREHEAD & FEENER 1998, BESTELMEYER 2000), body sizes (KASPARI 2005), morphological castes and polydomy (DEBOUT & al. 2005) at a global scale.

Studying ecological traits of ants will lead to advances in understanding ecology in general. But it becomes especially important to know more about global patterns and correlations of ant characteristics in the light of on-going global changes. Notably climate change and biological invasions are both predicted to have enormous consequences for biodiversity (BELLARD & al. 2012, SIMBERLOFF & al. 2013). But species' vulnerability to these drivers of species' extinctions depends in part on the species' ecological traits (FODEN & al. 2008). Yet, in order to make predictions and quantitative assessments, global patterns need to be investigated (ANGERT 2011). With a large-scale database of ecological characteristics of ants, it becomes possible to test for global patterns.

A similar database on ecological and morphological traits of plants, LEDA (KLEYER & al. 2008), has been cited in 70+ publications on diverse subject areas, aiming to understand life-history strategies and ecological mechanisms, using plants as a model system. For example, this database has been used to investigate the role of life-history traits in ecosystem functioning (THOMPSON & al. 2005), species survival (SOONS & OZINGA 2005) and plant distributions in fragmented landscapes (ENDELS & al. 2007).

Currently, several excellent ant databases exist, including Antweb (FISHER 2012), Antbase (AGOSTI & JOHNSON 2005), Ants of Africa (TAYLOR 2010), Japanese ant image database (JAPANESE ANT DATABASE GROUP 2003), NZ landcare (LANDCARE RESEARCH 2012), Ants of North America (MACKAY & MACKAY 2003), Fourmis de France (WAGENKNECHT & al. 2012) and Encyclopedia of Life's (EOL) section on ants (WILSON 2003, KAUTZ & MOREAU 2011, ENCYCLOPEDIA OF LIFE 2012). Generally, the main focus of these databases is on species morphology and distribution. Additional information on the species ecology, e.g., habitat, nesting requirements or species interactions, is usually presented in form of a brief description. This ecological description of a species' ecology does not, however, follow a general structure, as it is classically the case for the descriptions of taxonomic characteristics in the databases mentioned above. Although, much information exists on the ecology of ants, it is dispersed in books, publications, and much exists in the form of personal knowledge of myrmecologists, unpublished datasets and the databases men-

tioned above. The lack of a standardized database of ant ecology makes it impossible to access and analyze this existing information in a quantitative way. Therefore, we decided to set up a global database of ecological characteristics of ants with the aim to offer this possibility to the scientific community. "Ant Profiler" (<http://www.antprofiler.org>), is the only database providing a structured and standardized ecological "profile" for each species, which can be directly used in global as well as comparative studies. The aim of the database is to become a public research tool that relies on the contribution of myrmecologists.

### Description of the database

For each species, a "profile" is created that contains the available information on 24 basic ecological characteristics (Appendix 1, as digital supplementary material to this article, at the journal's web page). The information is presented like an ID-card, in form of a list of all categories and the value corresponding to each of these categories (Fig. 1). We included information on: (I) species occurrence (ecozones, distribution by country, habitat types, nesting types, association with disturbance, invasiveness status); (II) species morphology (min. and max body size, worker polymorphism, sterile / egg-laying workers, presence of a sting); (III) colony dynamics (polygyny, colony structure, colony density, colony size); (IV) behaviour (diet, aggressiveness, foraging behaviour, activity range); and (V) species interactions (symbioses, parasitism, nest-raids, slave-making species). According to the type of data, the values of the characteristics can be binary, quantitative, mutually exclusive or multiple-choice (e.g., "habitat", as a species can be present in different habitat types).

At the end of the species' profile, references can be associated with each contribution. Published work from journals or books can be linked to one or several of the characteristics, so that the information in the database can be retraced to its original source. However, in order to avoid losing existing but unpublished information, it is also possible that myrmecologists indicate that the information is a "personal observation" and thereby they become the reference for the value they contributed.

### Searching for information

The main specificity of our database is that it allows one to search for species with certain ecological characteristics (Fig. 2). We developed a search interface, which enables the user to search for all species corresponding to a certain trait (e.g., predatory species) or combination of traits (e.g., predatory species living in rainforests). To make searches easier, users can select the value of the trait that they are interested in and select a search link; in that way the user can select not only species corresponding exactly to a certain characteristic, but also species that have, for example, colony sizes that are "equal to" or "greater than" a certain numerical value. It is also possible to search for characteristics within a genus or a geographic area.

Furthermore, it is possible to search for traits of any given species by consulting its profile. This can be especially interesting for local investigations that aim to know all the traits of all species found in a specific site. Similarly, it is possible to search for traits within a given genus by accessing each of the species profiles that are all provided by one single request.

Fig. 1: Example of the first part of a species' profile.

In addition, the asset of this database structure is that it allows statistical analyses, such as correlations between any pair of traits or even more complete, multivariate analyses. The whole dataset can be downloaded as an excel file and data can be directly analyzed, opening the possibility to answer an endless number of questions (e.g., Fig. 3). As a first step, the access to the information, in form of a spread-sheet, will be restricted to significant contributors of the database.

### Data contribution

Ant Profiler is an online database, which relies on the contribution of myrmecologists, who have to register in order to add information to the database. An author can either "create" a new species-profile, which does not already exist in the database, or contribute lacking information for an existing species. Each piece of information is linked to the name of the contributing author so that all contributions can be retraced to their author. The "history" of each profile is also displayed, enabling the user to consult the date at which new information has entered the database as well as the author and date of subsequent modifications. At present, approximately 30 authors are registered and more than 2000 profiles of ant species have been entered. This already represents 13.5% of described ant species in the Bolton catalogue (BOLTON & al. 2007). The number of species created can be visualized on the main page of the database.

### Conclusion

Ant Profiler is a database of ant species that includes 24 basic ecological characteristics and that allows to search any species corresponding to a certain characteristic or combination of characteristics. The database includes quantifiable

ecologie  
systématique  
Evolution

Search:

Country Equals France ✓  
Diet IsDifferent Omnivorous ✓  
WorkerPolymorphism Equals Yes ✓  
Sting Equals Yes ✓

Franck Courchamp  
[Log Out]

3 results Show 10 per page

Name	Gyny	ColonyDensity	Workers	WorkerPolymorphism	MinBodySize	MaxBodySize	SterileWorkers	Sting
<i>Pheidole pallidula</i>	Monogynous	Abundant		Yes	2	4		Yes
<i>Messor bouvieri</i>	Monogynous			Yes	4	8		Yes
<i>Messor wasmanni</i>	Monogynous			Yes	3	9		Yes

ANT PROFILER

Fig. 2: Search interface allowing the user to search for all species in the database presenting any particular trait or combination of traits. It is possible to access any of the profiles of these species.

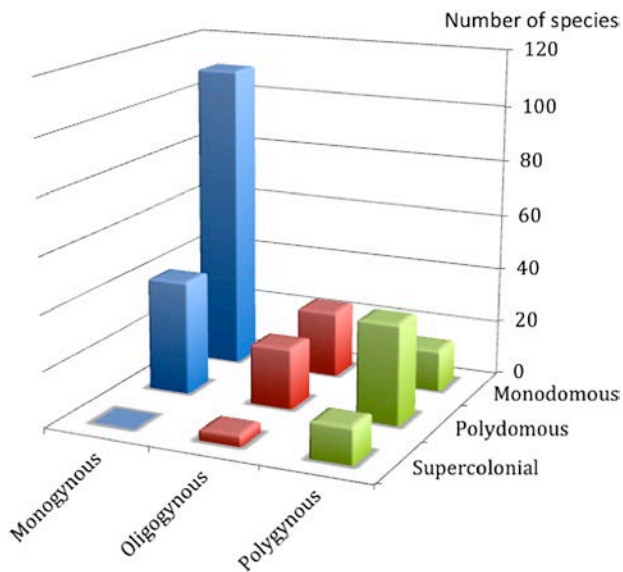


Fig. 3: Relationship between nest structure and the number of queens as an illustration of a possible question that could be investigated with the Ant Profiler dataset.

information on ants that can also be analysed statistically. At this stage it is crucial that a collective effort from the myrmecologist community is made to contribute data – or datasets – in order to fill up the database. This quantitative approach has the potential to lead to the discovery of new patterns and to new understanding of the ecology of ants, and beyond of other organisms. If all specialists were each to create a few profiles, the resulting richness of the collective knowledge would far surpass the sum of its compo-

nents, allowing virtually boundless possibilities of questions, searches and analyses, for an incomparably improved knowledge of ant ecology.

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Myrmecological News	18	Digital supplementary material
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## Digital supplementary material to

BERTELSMEIER, C., LUQUE, G.M., CONFAIS, A. & COURCHAMP, F. 2013: Ant Profiler – a database of ecological characteristics of ants (Hymenoptera: Formicidae). – Myrmecological News 18: 73-76.

Appendix 1: Structure of the Ant Profiler database. The 24 characteristics and possible values are listed within five trait categories.

	Trait	Values	Option	Information
Colony dynamics	Gyny	Monogynous		
		Polygynous		
		Facultative		
	Colony structure	Monodomous / Monocalic		
		Polydomous / Polycalic		
		Supercolonial		
	Colony foundation	Independent		
		Dependent		
		Facultative		
	Colony density	Abundant		
Medium				
Rare				
Colony size	Count			
Morphology	Worker polymorphism	Yes		Whether or not morphologically different worker casts exist
		No		
	Min body size	Size in mm		Smallest workers
	Max body size	Size in mm		Biggest workers
	Sterile workers	Yes		Whether or not the workers are able to lay eggs under certain circumstances
		No		
Sting	Yes			
	No			
Behaviour	Diet	Scavenger	Multiple choice possible	
		Granivorous		
		Predatory		
		Fungus-growing		
		Honeydew / EFN		
		Omnivorous		
	Aggressiveness	Aggressive		Most common level of aggressiveness in the focal species
		Unresponsive		
		Evasive		
	Activity range	Day		
Night				
Day and Night				
Foraging behaviour	Mass recruiter	Multiple choice possible		
	Group hunter			
	Solitary forager			

Species interactions		Fungus grower		
		Army ant		
		Homopteran tender		
	Symbioses	Yes	Name of symbiont	
		No		
	Parasitic species	Yes	Name of parasitized species	
		No		
	Slave-making species	Yes	Name of slave species	
		No		
	Nest-raids	Yes	Name of raided species	
No				
Occurrence	Habitat	Rainforest	Multiple choice possible	
		Boreal forest		
		Temperate forest		
		Tropical dry forest		
		Grassland		
		Riparian zones		
		Desert		
		Coastland		
		Shrubland		
		Tundra		
		Urban areas		
		Agricultural areas		
		Generalist		
	Nesting type	Tree / Canopy	Multiple choice possible	
		Leaf litter		
		Ground		
		Twigs and Logs		
		Underground		
		Ubiquitous		
		Nomad		
	Disturbance specialist	Yes		Whether the species nests frequently in disturbed habitat
		No		
	Invasiveness status	Native		The species has no known established populations outside its native range
		Exotic / Tramp		The species has established populations outside its native range
		Invasive		Exotic species with ecological impact on native species
	Ecozone	Afrotropical	Multiple choice possible	
		Palaearctic		
Holarctic				
Nearctic				
Neotropical				
Indomalayan				
Oceanic				
Australasian				
Cosmopolitan				
Distribution	Name of countries			

# Characteristics of invasive ants

Cleo Bertelsmeier, Sébastien Ollier and Franck Courchamp





# 16. Characteristics of invasive ants

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## 1. INTRODUCTION

Since their origin about 120 million years ago, ants have evolved to become the most-species-rich and ecologically diverse group of social insects <sup>1</sup>. Currently there are more than 12,500 described species of ants but there are many species remaining to be discovered and it has been estimated that their actual number could well exceed 25,000<sup>1</sup>. Unfortunately, many of the places that could harbour the greatest levels of ant diversity are also the least explored and studied, such as West Africa, southeast Africa, North East Brazil, Mexico or New Guinea <sup>2</sup>. Because of their ubiquity in a great diversity of habitats on all continents (except Antarctica) <sup>3</sup> and their small body size, ants are easily transported by accident <sup>4</sup>. In addition, they are often associated with urban or agricultural landscapes and are often found on ornamental plants, fruits or other fresh products and timber <sup>4</sup>. In total, more than 250 species have been recorded outside of their native ranges <sup>5</sup> but it has been estimated that there are actually more than 600 introduced ant species worldwide <sup>6</sup>. Among these several hundreds exotic ants, a small number has become invasive, *i.e.* the introduction has been followed by a demographic explosion and the species causes impacts on native biodiversity and/or human health. The Invasive Species Specialist Group (ISSG) of the International Union for the Conservation of Nature (IUCN) lists 19 ant species as highly problematic <sup>7</sup>, and 5 are even on the list of the “100 of the worst invasive species” <sup>8</sup>.

Ant invasions can cause the local extinction of a variety of native species, including many arthropods, plants, birds, herpetofauna and mammals <sup>9-11</sup> and disrupt ecosystem functioning <sup>3,12-14</sup>. Economic losses can be high due to the destruction of agriculture, damages to property (cars, TV, electrical wires, telecommunication...) and the infestation of human estates <sup>15</sup>. The estimated total annual cost for a single species of fire ant, *Solenopsis Invicta*, is between one <sup>16</sup> and six <sup>17</sup> billion dollar in the US alone. In addition, more than 200,000 people per year need medical treatment in the US after being stung by invasive ants <sup>11</sup>. The disease-carrying potential of invasive ants has also been highlighted <sup>18</sup>, as a variety of different pathogenic agents are carried by invasive ants in hospitals, likely causing a wide range of serious infections <sup>19</sup>.

Once invasive ants become established in a climatically suitable area, it is very difficult to control or eradicate them <sup>20</sup>. If an invasive species has already spread over a large area and reached a high population density, successful eradication becomes more and more unlikely – if not entirely infeasible <sup>21</sup>. In general, reactive programs have proved far more expensive than proactive programs <sup>22</sup>. However, species-specific protocols are needed before taking action <sup>20</sup>. Therefore, assessments have been made that rank species and areas according to their level of invasion risk <sup>20,23,24</sup> (chapter 9). An important limitation of these assessments is that they can only take into account species that are already known to be invasive somewhere and that have caused notable impacts. Yet, it is known that the number of species introductions is continuously rising with increasing tourism and commercial exchanges <sup>25</sup>. In fact, the number of invasions could increase exponentially in the future due to a time lag between the first introductions and actual invasions <sup>25</sup>. Therefore, it would be extremely useful to develop a tool to identify

future potential invaders<sup>24</sup> in advance based on a certain number of biological traits. Invasive ants are thought to share a certain number of ecological characteristics contribute to their ‘invasive syndrome’ related to their habitat preferences, behaviour, colony structure or reproduction<sup>9-11</sup>. Nonetheless, this ‘invasive syndrome’ has rarely been studied in a quantitative way. One widely known study compared the body size of 78 non-native with 78 native congeneric species and found that introduced species were, on average, smaller than native species<sup>26</sup>. Another study on 147 introduced species found that more than 50% belong to the subfamily *Myrmicinae*, which is the most species-rich subfamily in ants and are disproportionately more often of Neotropical or Oriental biogeographic origin<sup>5</sup>. Another study analysed ecological traits of native and introduced ant species in North America<sup>27</sup> and found that a larger colony size was the only trait consistently associated with introduced ants. However, all previous studies concentrate on a small subset of species (e.g. North American ants) or traits. So far, no comprehensive “profile” of invasive ants has been described in a quantitative way.

This is why we set up the Antprofiler trait database<sup>28</sup> with 24 ecological traits on ants worldwide (Chapter 15). The data-gathering phase of this ambitious project has been running for over two years now and is still on-going. I will present in this thesis chapter the current content of the database and a preliminary analysis. I will then briefly discuss the perspectives for further analyses and the development of a predictive framework for ant invasions.

## 2. MATERIAL & METHODS

### *Species*

The Antprofiler database (described in greater detail in Chapter 15) contains at present 2193 species and information on 23 traits (Fig. 1), which can be separated into three types of data: quantitative, qualitative and multiple-choice. Quantitative traits contain information on minimum and maximum body size and on colony sizes. Qualitative traits include data on polygyny, colony structure, type of colony foundation, colony density, worker sterility, presence of a sting, level of interspecific aggressiveness, daily activity range, symbioses, parasitism, slave-making, nest raids, association with disturbance and the invasiveness status. Multiple-choice traits contain information on diet, foraging behaviour, habitat, nesting type and ecozone.

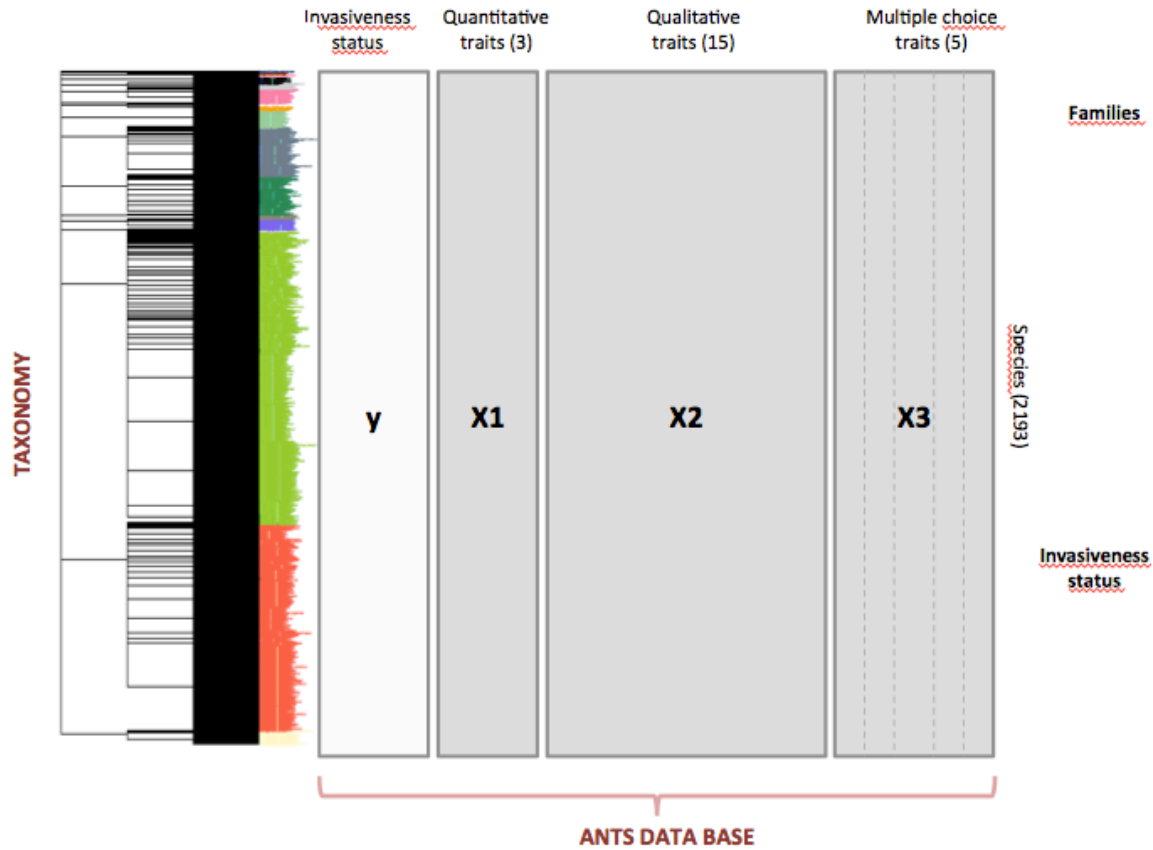
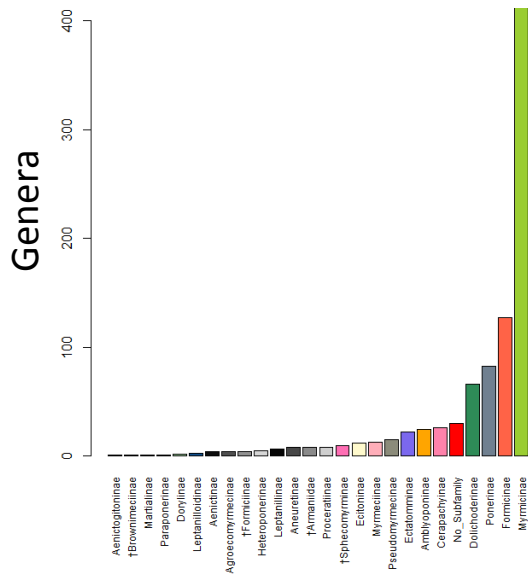


Fig. 1 Structure of the database. Lines represent individual species profiles (in total 2193) and columns are traits. The corresponding subfamilies have been associated with each species (left) based on data from Antweb. Each species has an invasiveness status, and data on different quantitative, qualitative and multiple-choice traits.

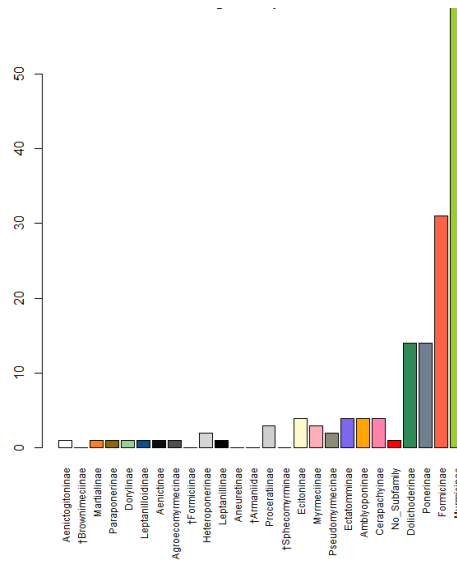
*Phylogenetic information*

We linked the species data in Antprofiler to taxonomic information on the subfamilies and genera from the authoritative database Antweb <sup>29</sup>, which contains data on all known 26 subfamilies and 909 genera; but less than 300 extant genera. Antprofiler includes 154 ant genera from 21 subfamilies. The distribution of the genera in Antprofiler is coherent with Antweb (Fig. 2) without any strong biases towards particular subfamilies.

Antweb (>15,500 species)



Antprofiler (2,193 species)



Subfamilies

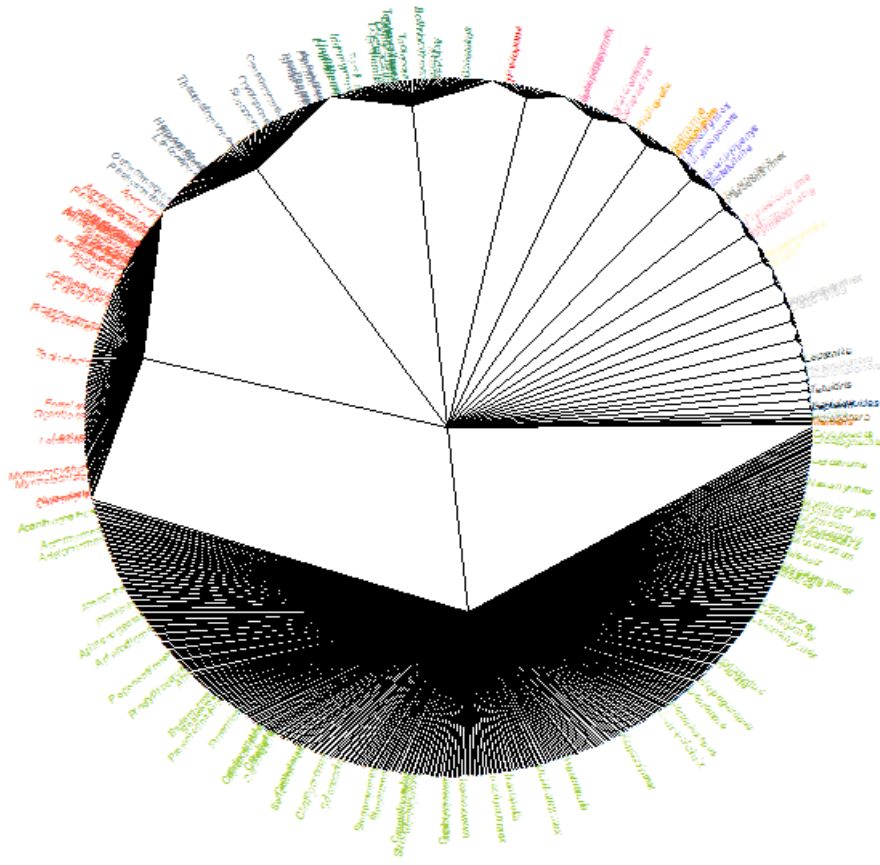


Fig. 2 Representation of genera per subfamily in the taxonomically comprehensive database Antweb (left) and in Antprofiler (right). The distribution of genera in Antprofiler within the taxonomic classification of Antweb is shown on the bottom.

The only published ant phylogeny contains 293 ant species distributed across 166 genera<sup>30</sup>. Out of these species, 98 are present in our Antprofiler database, which are distributed relatively regularly across the phylogeny of Moreau et al.<sup>30</sup> (Fig 3)

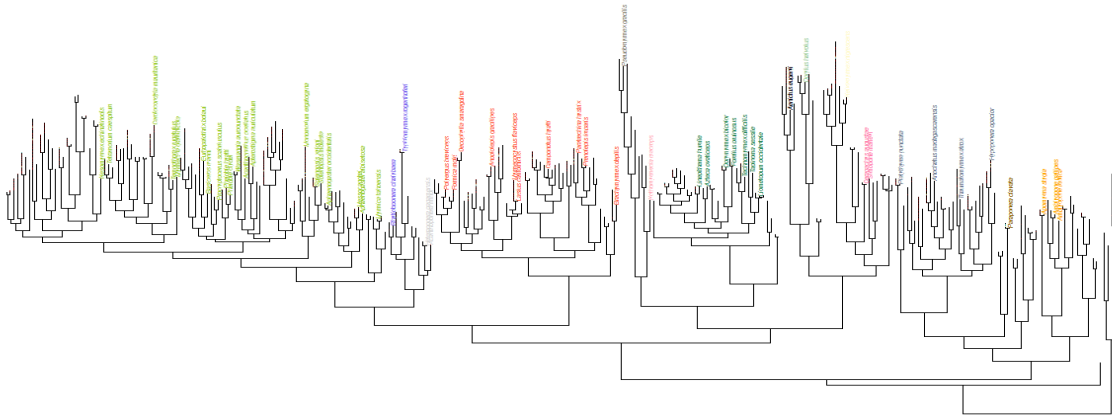


Fig. 3 Ant phylogeny published by Moreau et al.<sup>30</sup>. Branches in colour are species present in the Antprofiler database.

*Missing data*

For 70% of the 2193 species more than 2/3 of the trait data is missing, only 5 species have data on all 23 traits and 11% of the species have data on at least 2/3 of the traits (Fig. 4). Most species have information on 3-7 traits. However, the amount of data available differs greatly among the traits. More than 50% of the species have data on their ecozone, habitat and worker polymorphism. The least well-known traits are colony density, interspecific aggressiveness and activity range (Fig. 5).

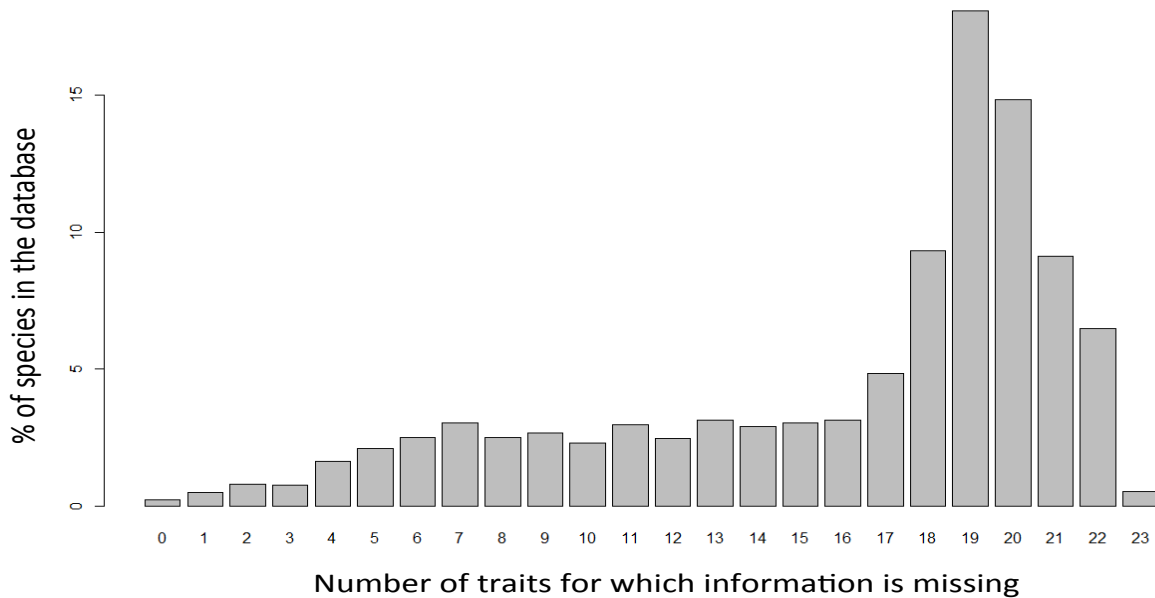


Fig. 4. Distribution of missing data in the Antprofiler database.

The unequal data quality on different traits is explained by the fact that most ant species are not very well known. In fact, many ant species are known from a few museum specimens that are kept in ant collections. Collectors have often recorded the locality, the habitat and perhaps the type of nest where they found the ants <sup>29</sup>. On the other hand, behavioural data are more difficult to obtain, as they require observation of these species. Given that the missing information is not randomly distributed in the dataset, one could choose strategically among the 23 traits and/or the 2193 species of the database (Fig 5). For example, it is possible to minimize the missing information by selecting traits and species for which much data is available (upper right corner in Fig 5).

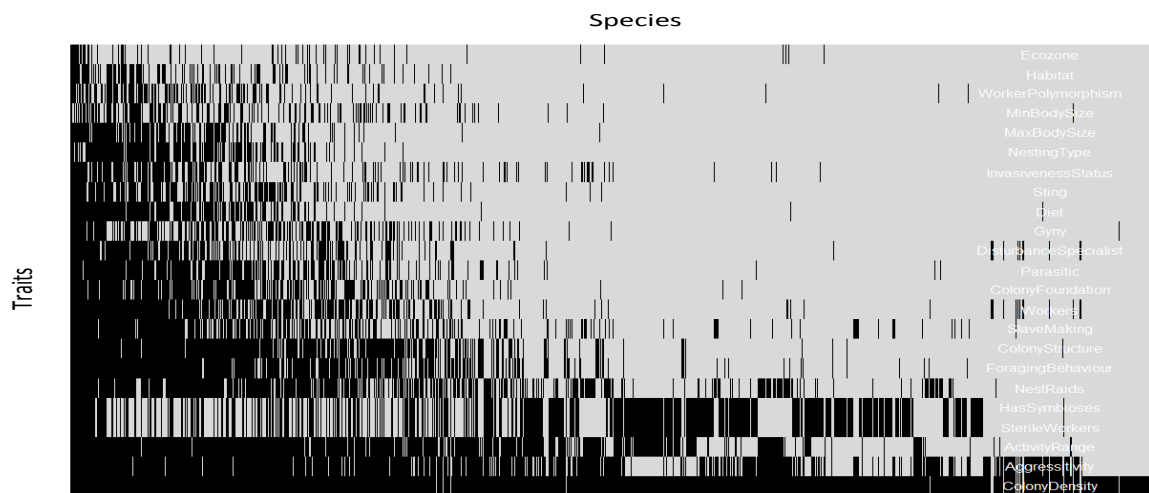


Fig. 5 Information on missing values in the trait database. The 23 lines represent the traits and 2193 columns are individual species. On the right, we represent species with little missing data; on the left, species with much missing data. Black bars stand for absent information, grey bars for present information.

#### *Invasive species trait analysis*

For the analyses of traits discriminating among native, exotic and invasive ants, we used a sub-sample of 55 species for which we had all data on quantitative and multiple-choice data and less than 4 absences in the qualitative trait (Fig. 6). The missing data are replaced by the mean profile of each factor. Among the species retained for the analysis, there was no taxonomic clustering of native, exotics or invasives in specific genera (Fig. 6).

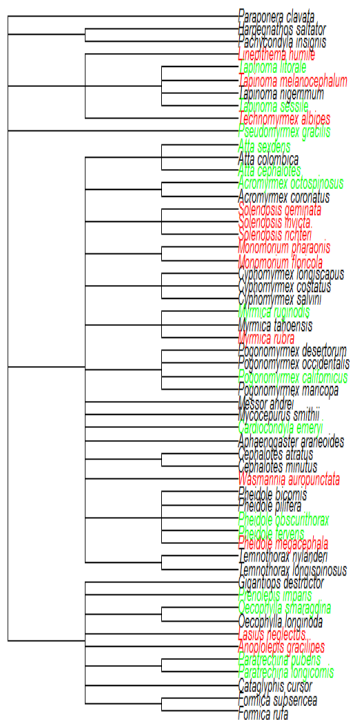
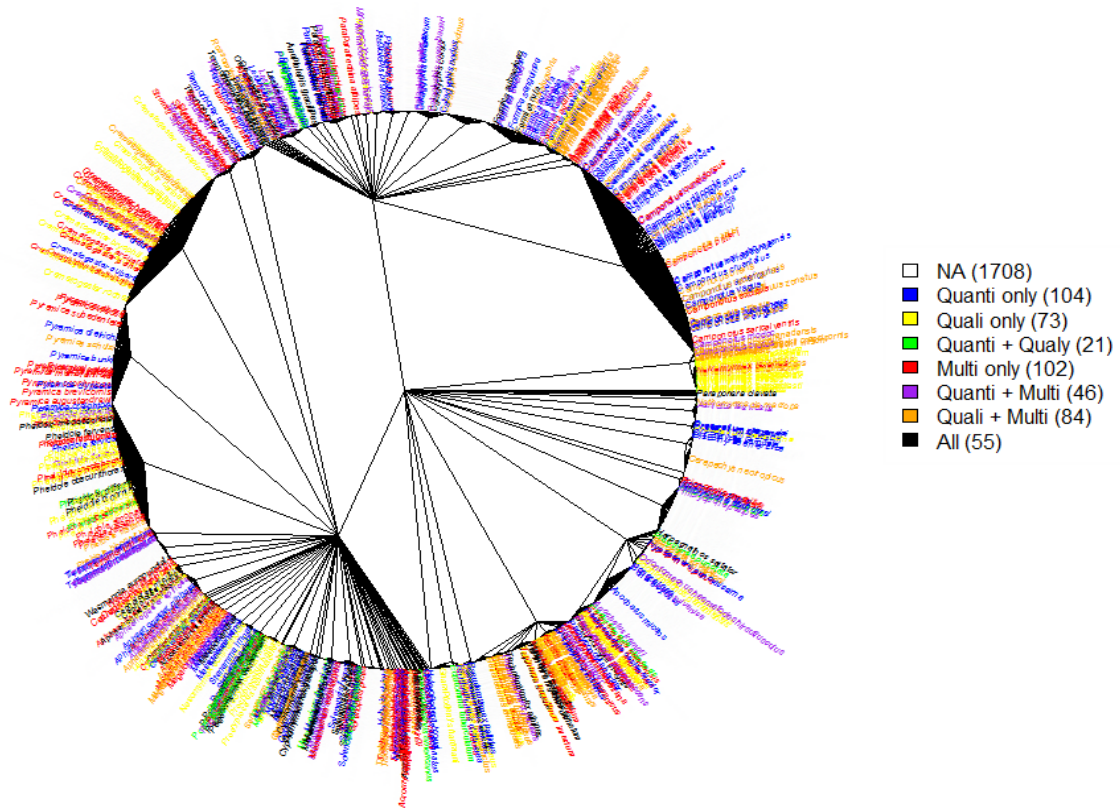


Fig. 6 Upper part: Subfamilies of species for which all data is available for quantitative traits (blue), qualitative traits (yellow), multi-choice (red) or different combinations of these. Lower part: 55 selected species that have sufficient data on all three categories to conduct multivariate analyses. Red: invasive, green: exotic, black: native species.



Comparisons were done among groups of native (Fig. 6, black), exotic (Fig. 6, green) and invasive ants (Fig. 6, red). We conducted three separate multivariate analyses according to the type of variable to see if variability allowed discriminating between the three groups. We carried out a Principal Component Analysis (PCA) with quantitative traits (colony size and maximum and minimum body size). Qualitative data was analysed using a Multiple Correspondence Analysis (MCA). Multiple-choice data (e.g. habitat type) was transformed into several binary variables that represent the modalities of the multiple-choice variable. For example, in the case of habitat, each modality (desert, rainforest, urban areas...) became a variable for which the value is either 0 or 1. We then conducted a PCA per multi-choice variable.

Finally, we combined the three separate analyses, by keeping the value of the coordinates on the first axis of the PCA of multiple-choice data and coordinates on the first axis of the MCA as well as the first two coordinates of the PCA on quantitative variables. Consequently, we obtained eight quantitative scores that could be analysed by a single global PCA.

### 3. RESULTS

#### Quantitative data

The first two axes of the PCA with the three quantitative variables discriminate the different clusters of invasive (red) and native (black) species – with a group of exotics in between (Fig. 7). The number of workers (colony size) is almost orthogonal to the two body size variables (min and max body size). Both axes contribute to discriminate clusters.

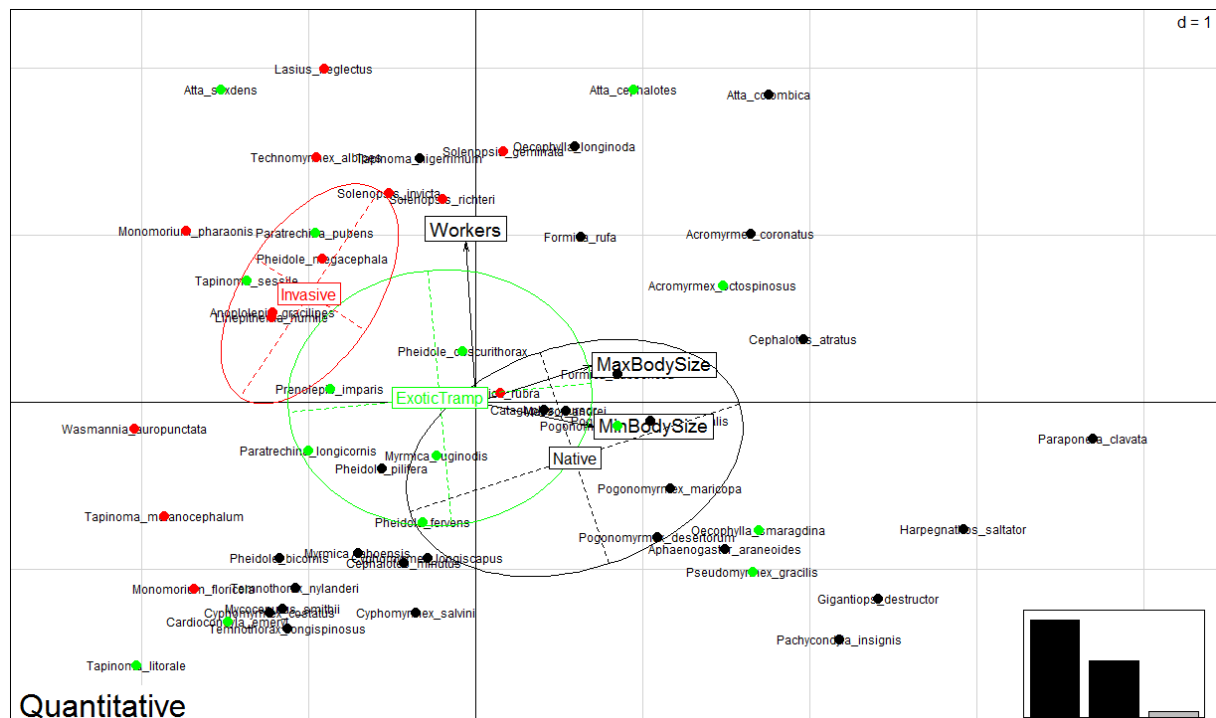


Fig. 7 Biplot of the PCA on the 3 quantitative variables table. Red cluster : invasive species, green cluster : exotic species, black cluster : native species.

Qualitative data

The MCA with 15 qualitative traits shows a similar pattern with three distinct groups that are well described by the first axis alone. The invasive and native groups cluster at two extremes of a spectrum, with the group of exotic species in between (Fig 8a). The variables that contribute most to the differentiation of the groups along this axis are nest raids and supercolonial colony structure (Fig. 8b)

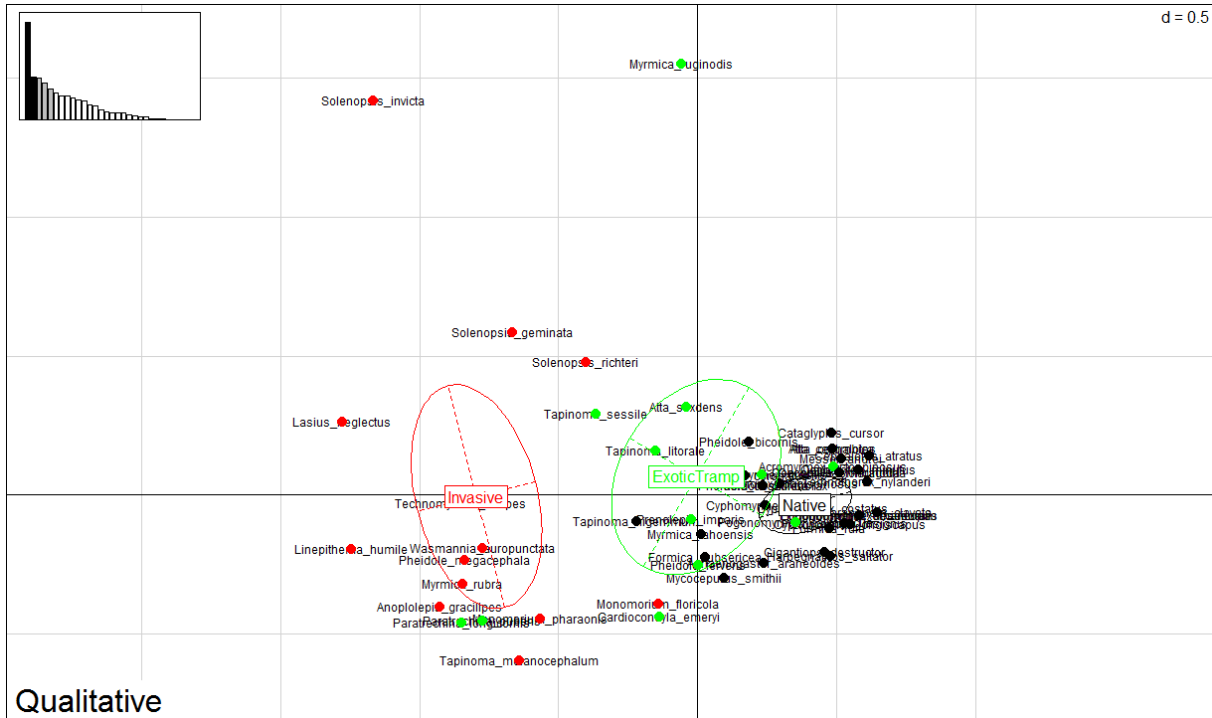


Fig. 8a Scatter plot of the MCA on the 15 qualitative variables table. Red cluster : invasive species, green cluster : exotic species, black cluster : native species.

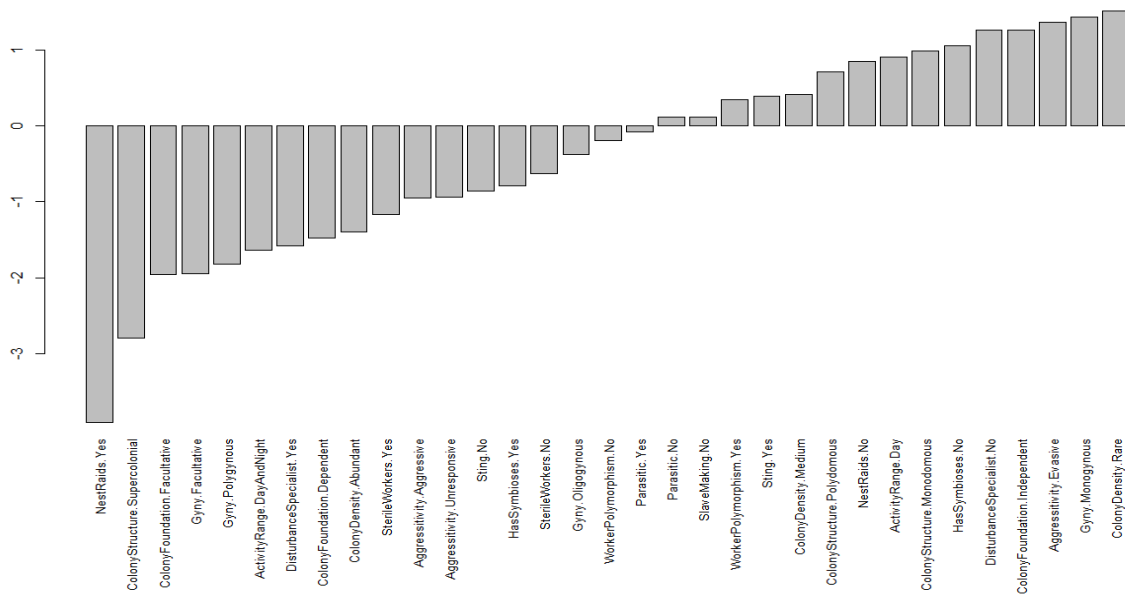


Fig 8b Barplot of factor coordinates on axis 1.

Multiple-choice data

PCAs with all five multiple-choice traits (ecozone, diet, foraging, habitat and nesting) show again a separation of the three groups (native, exotic, invasive) (Fig. 9).

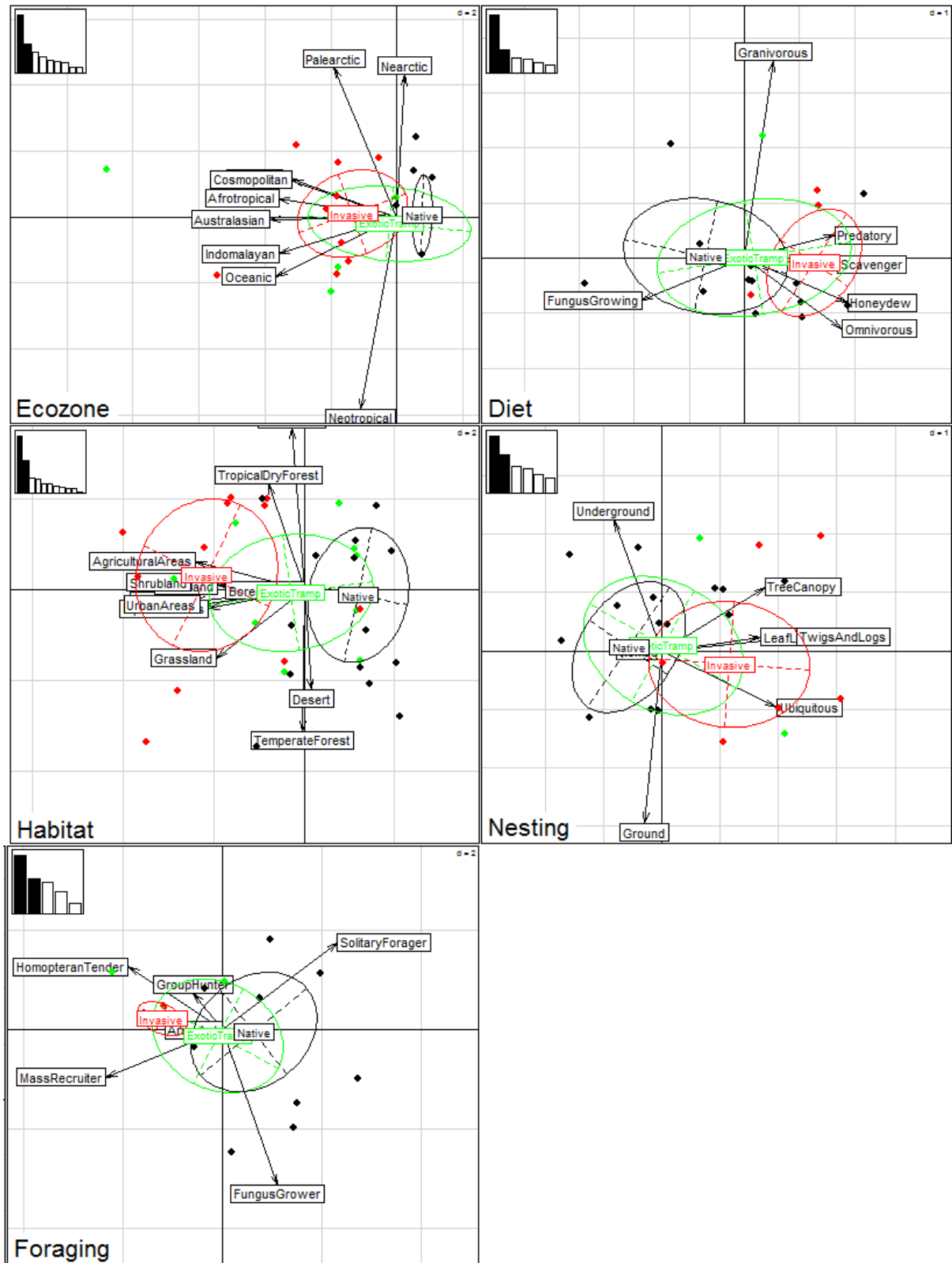


Fig. 9 Biplots of the five PCA on multiple-choice variables. Red cluster : invasive species, green cluster : exotic species, black cluster : native species.

## Global PCA

The global PCA combines the coordinates on the first axis of the PCA with multiple-choice variables, the coordinates on the first axis of the MCA with qualitative variables and the coordinates on the first and the second axes of the PCA with quantitative variables (in the case of quantitative variables we took the first two axes because both axes contributed substantially in distinguishing invasive from native species) (Fig. 10a). The pattern is very clear; there are three distinct clusters of native, exotic and invasive species. Native species have negative coordinates on axis 1 while invasive species have positive ones. However, some exotic species are within or near this group. All groups of variables contribute to discriminate clusters but the score *Quanti2* (which is particularly correlated to colony size, Fig. 7) seems to play an original role.

We mapped the coordinates of each species on axis 1 of the global PCA in front of the taxonomy of Antweb (Fig. 9b, left). Although invasive species are not clustered within one group, there is a phylogenetic pattern as positive and negative coordinates on the axis 1 of the global PCA appear in 'blocks' (Fig. 10b, right). These blocks at the genus level would be even stronger, if the 'exotic' species with positive coordinates (i.e. classified within the cluster of the invasive species) turned out to be actually invasive species.

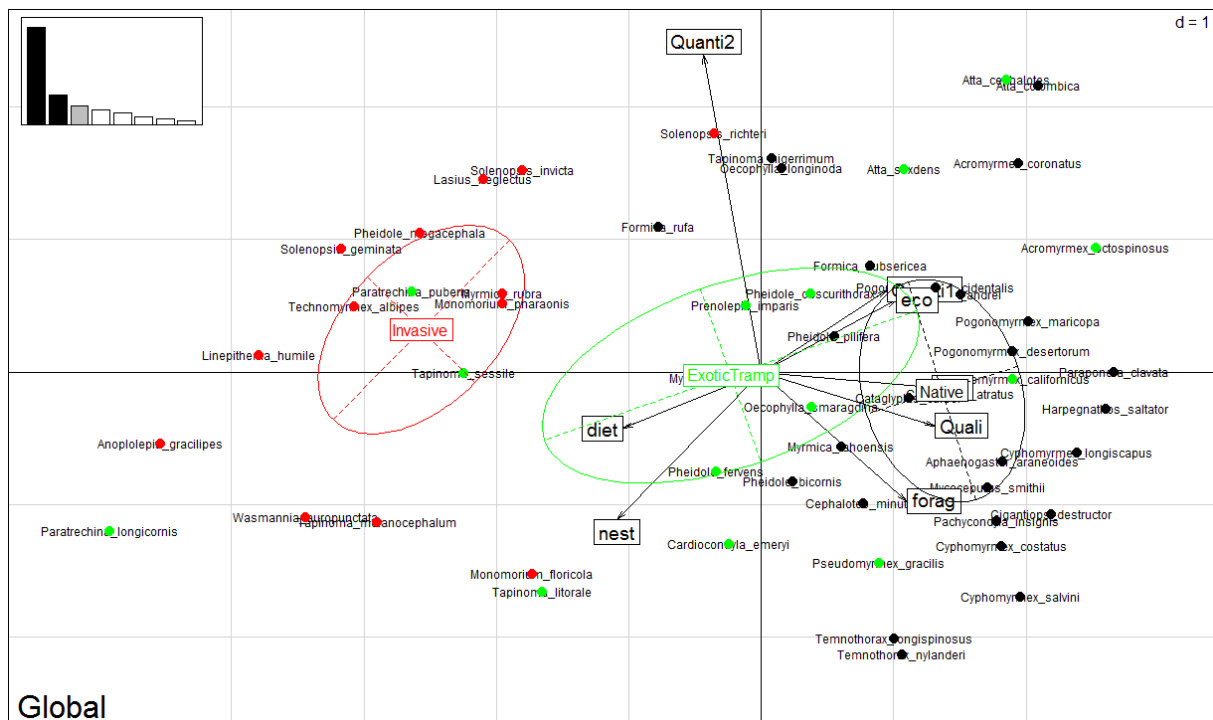


Fig. 10a Biplot of the Global PCA. Eco=ecozone, hab=habitat, forag=foraging, nest=nesting type, quanti1=first axis of PCA on quantitative variables, quanti2= second axis of PCA on quantitative variables, quali= first axis of MCA on qualitative variables.

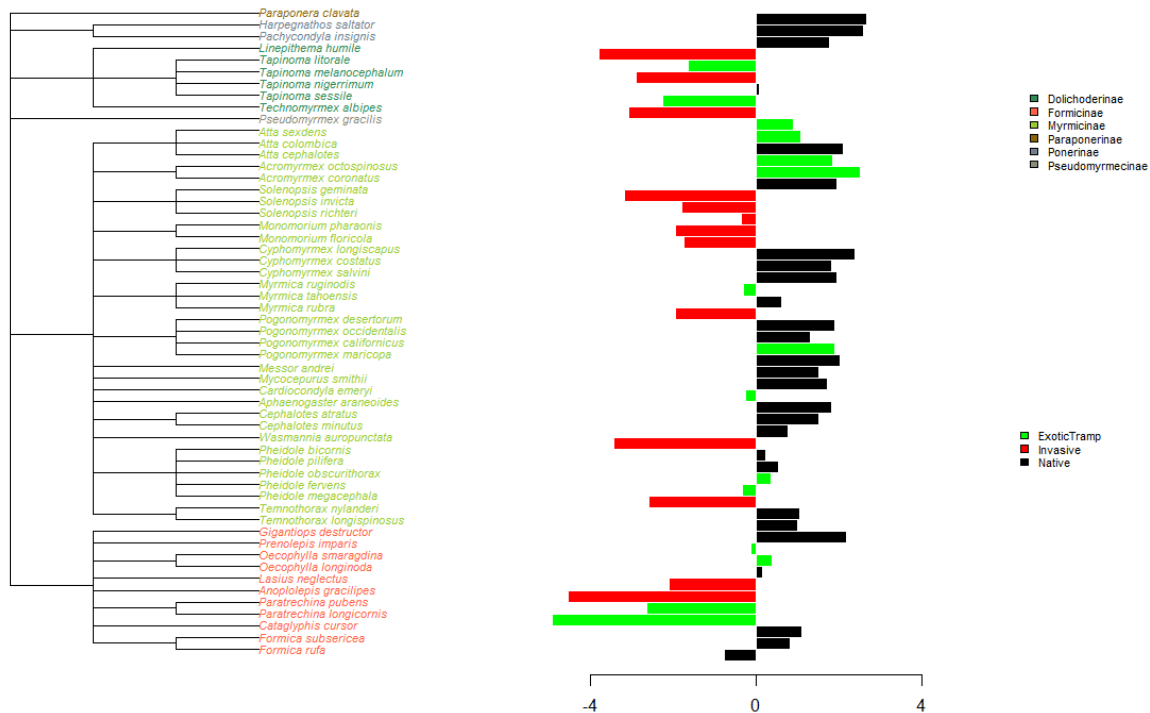


Fig. 10b Combination of the ant taxonomy of the 55 species (left, colour indicate different subfamilies) and their coordinates on the first axis of the global PCA (right, black= native, green=exotic, red=invasive).

Species among the invasive species cluster could have a high probability of becoming invasive at a later stage. Our analysis identified 4 main candidates: 1/ *Paratrechina longicornis*, which is actually invasive, but which we had left out before the analysis, which it has correctly classified it as invasive, 2/ *Paratrechina pubens*, the Caribbean crazy ant, which is already a major pest in the Caribbean islands where it causes serious crop damage<sup>31</sup>, 3/ *Tapinoma littorale* and 4/ *Tapinoma sessile*. This species is called the odorous house ant because it emits a blue-cheesy odour when crushed and often forages in great numbers inside houses. It has already been suggested that this ant might successfully invade other temperate areas in the future, which are outside the US<sup>32</sup>.

#### 4. DISCUSSION

Currently there are 2193 species from 154 genera and 21 subfamilies in the AntProfiler database. The sample does not display a strong phylogenetic bias. We chose a subsample of 55 species for which we had sufficient data to conduct multivariate analyses with the 23 ecological traits in the AntProfiler database. All multivariate analyses with quantitative traits (PCA on 3 traits), qualitative traits (MCA with 15 traits) and multiple-choice traits (PCAs on 5 traits) showed a strong pattern in the data with three clearly distinct groups: native, exotic and invasive species. The global PCA that combined data from all three analyses showed a very strong structuration by the first axis, with the non-overlapping 'native' and 'invasive' groups at the two extremes of the axis and the exotic group in between. Four species classified here as 'exotics' have been identified as strong candidates to be invasive species. One of them is actually an invasive species, which we had labelled 'exotic'. This gives support to the analysis being able to correctly identify potentially invasive species. Among the three other species *Paratrechina*

*pubens*, *Tapinoma littorale* and *Tapinoma sessile*, two are serious pests and are thought to be potentially invasive<sup>31,32</sup>.

A limitation of this preliminary approach is that it is based on a sub-sample of only 55 species. We could have analysed different (greater) sub-samples for which we have data on all quantitative, qualitative or multiple-choice variables for example. But in that case, we could not have combined them in a single global PCA, which demonstrated that the 'invasive syndrome'<sup>9-11</sup> is clearly an ecologically coherent group, structured along the first axis. Similarly, we could have carried out univariate test for single variables for which we have a great amount of data, but the problem here is that correlations between different variables can go undetected. In addition, if one analyses different sub-samples, the relationships and correlations between different variables could differ from one sub-sample to the other. Therefore, it is not clear if a statistical association of a certain trait with invasiveness would hold true for a different sub-sample.

We currently aim to fill the database in a strategic way by trying to contribute first the missing information for species that have already a lot of trait information – so that they could be added to the multivariate analyses. Another possibility is to choose a subset of the ecologically most relevant traits for which information is abundant (Fig. 6). Furthermore, some traits may be relatively easy to complete in the future. For example, rare traits such as 'slave-making' are mentioned in the literature only when they are present, and obviously not if there are absent. But if the person filling out a species' profile was unsure about the species' status, he or she would not put any information although the species would very likely not be a slave-making species. In the future, we could try to get a comprehensive list of all slave-making ants for example from a reliable expert opinion on this particular trait and attribute the non slave-making status to all other species. In addition, under some circumstances the holes in the dataset could be filled by inference algorithms that base their estimation on known relationships between the focal trait and other traits in the database. These methods work best for traits for which a lot of information is already available in the database (so that the relationships between this and other variables are reliable) and could be used to infer a small number of holes. But this may have a greatly increase the number of species that could be added to the final multivariate analysis.

Further, for the purpose of these preliminary analyses, we have presented the taxonomy and phylogeny of the ants side by side with the content of the Antprofiler database to show that our sample is not strongly phylogenetically biased. However, some ecological traits are clearly associated with the phylogeny and in future analyses, it would be interesting to take it into account. Here, we would have to decide whether to include the phylogenetic information of the Moreau et al. classification<sup>30</sup> and restrict our sample to our 98 species included in this phylogeny. Alternatively, we could restrict the analysis to the subfamily/genus level provided by the taxonomic information in Antweb, which would cover all species in our database but be less precise.

As a next step, following the descriptive analysis of the dataset, we plan to develop a predictive model on invasiveness in ants (perhaps a GLM). The idea is to predict the probability that a given species might become invasive, based on its ecological characteristics. Our preliminary analyses have yielded strong results and were able to discriminate well between the groups of native, exotic and invasive species. The ecological traits in the Antprofiler database have therefore a strong potential to be able

to predict future ant invasions. This would be extremely useful, given the current rate of ant introductions <sup>4</sup>, which is likely to lead to a steep rise of invasions in the future <sup>25</sup>. A predictive identification tool of potential invasive species could help prioritizing surveillance efforts at ports of entry for example <sup>20</sup>.

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## General Discussion



## 17. DISCUSSION

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Climate change<sup>1</sup> and biological invasions<sup>2,3</sup> are both among the greatest threats to biodiversity and their impacts might increase by the end of the century. On-going human development will release massive amounts of greenhouse gases into the atmosphere<sup>4</sup> that will continuously exacerbate climate change and increasing globalization including trade and tourism will lead to an increasing number of species introduced outside of their native ranges<sup>5,6</sup>. Among invasive species, ants (*Formicidae*) are a prominent group due to their enormous negative impacts on native species, ecosystem processes, human and animal health, agro-ecosystems and the economy<sup>7-9</sup>.

The objective of this thesis was to forecast future ant invasions – especially in the light of on-going climate change, which is generally thought to favour invasive species by removing thermal barriers. Here, I used three complementary approaches to study the potential of different ant species to invade in the future: 1/ bioclimatic species distribution modelling to assess potentially suitable landmass for 15 of the worst invasive ant species, 2/ behavioural experiments in the lab to rank different species according to their behavioural dominance and capacity to exploit resources and finally 3/ a trait database to identify characteristics of invasive ants that could be used in the future to identify new potential invaders.

The species distribution models showed a global increase of suitable climatic conditions for some species, such as the Asian needle ant, *Pachycondyla chinensis*, with especially large increases in Europe, Oceania and North America<sup>10</sup> (Chapter 5). The result is interesting because the species is a very recent invader and has been added to the ISSG database only last year<sup>11</sup>. However, invasive species can benefit from climate change not only by increasing their total suitable range but also if the relative suitability within their potential range (or ‘habitat quality’) increases<sup>12</sup> (Chapter 6).

Surprisingly, I found that, contrary to the general expectations, not all invasive ant species were likely to benefit from climate change and I illustrated that with a study on big-headed ants, *Pheidole megacephala*<sup>13</sup>. The species was predicted to decrease in range size and suitability on all continents and across all time horizons considered (Chapter 7). Comparing the potential ranges of 15 of the worst invasive ants for which I had sufficient occurrence data to build models, I found that there was no homogeneous trend (Chapter 8). Seven species decreased with climate change, five increased and three remained stable. This heterogeneity was seen on all continents, with several species increasing and many species decreasing. Under current climatic conditions, suitable areas for the 15 species considered clustered into large potential ‘invasion hotspots’, mostly in tropical and subtropical regions, which coincided well with the current biodiversity hotspots – regions of exceptional species richness and a high level of vulnerability<sup>14</sup>. In addition, within the biodiversity hotspots, the potential distributions of the 15 invasive ant species were predicted to greatly increase in the future. Overall, invasive ants are likely to remain an important threat and it is important to prioritize areas and species for surveillance efforts. I took France as a model system to demonstrate how different *départements* (French administrative units) and ports of entry (maritime ports and airports) can be ranked according to the suitable climatic conditions that they present for different species<sup>15</sup> (Chapter 9). This follows current

calls by the scientific community to apply species distribution models for concrete recommendations<sup>16-19</sup>. However, conservation actions taking into account climate change projections can be based on different time horizons in the future. This is why I studied the influence of the choice of the time horizon on projections by forecasting potential distribution for the 15 ant species in 2020, 2050 and 2080 (Chapter 10). I found that 6 out of 15 species showed 'trend reversals', i.e. that an initial increase of suitable areas was followed by a decrease or vice versa, illustrating the importance of making forecasts for several time horizons in the future to identify this type of patterns<sup>20</sup>.

In a field-based study, the model predictions were combined with an experimental approach, whereby artificial ant colonies were placed in the field to record survival under different environmental conditions and the results were consistent with the predictions (Chapter 11).

The species distribution models have identified large potentially overlapping distributions of several invasive ants. In the future, these species may arrive simultaneously in the same regions and compete with each other. In a series of experiments, I tested behavioural differences among 7 highly invasive ant species (*Anoplolepis gracilipes*, *Paratrechina longicornis*, *Myrmica rubra*, *Linepithema humile*, *Lasius neglectus*, *Wasmannia auropunctata* and *P. megacephala*). I discovered two different behavioural strategies among invasive ants (Chapter 12): The first group (*A. gracilipes*, *P. longicornis*, *M. rubra*) displayed evasive behaviour when individuals (1 vs 1 worker) or groups (10 vs 10) were confronted. On the other hand, the four remaining species were highly aggressive during encounters and formed a linear dominance hierarchy: *W. auropunctata* > *L. neglectus* > *L. humile* > *P. megacephala*. Interactions at the colony level, however, exhibited more complex demographic processes and more variability – although they were overall consistent with the dominance hierarchy established at the individual and group level (Chapter 13). Mimicking a scenario of multiple simultaneous invasions, I conducted a competition experiment with colonies of all four aggressive species simultaneously, adding another level of complexity that made results unpredictable. Further, I investigated resource competition among these four ant species, using two set-ups to test exploration of space with some spatial complexity and one set-up to test resource exploitation (Chapter 14). In both experiments, I found significant differences among species, with competitive abilities that were negatively correlated with their behavioural dominance.

Since there are more than 200 recorded exotic species of ants<sup>21</sup> and more than 600 estimated to have been introduced outside their native ranges<sup>22</sup>, it would be interesting to identify potential future invaders. In order to identify traits associated with invasiveness in ants, I set up a database with 24 ecological characteristics<sup>23</sup> (Chapter 15). I have worked for over two years collecting data of more than 2200 ant species. Nevertheless, there are many holes in the dataset because information is not always easy to find. Here, I have presented a preliminary simple analysis (Chapter 16) of trait differences between native and invasive ants that already point to clearly different clusters of invasive and native species, with exotic species somewhere in between. This is work in progress and it will result in the construction of a predictive model of the probability that a given ant may become invasive in the future, based on its traits.

As this manuscript is essentially a publication-based thesis, all research papers have their own discussion. This is why I will try to avoid repeating the technical parts of the discussions and specific caveats of single studies here. Instead, I would like to address some more general questions here involving each of the three approaches and to put the study results in a more general context, which I will mostly illustrate with examples from my modelling studies. I will start by the overarching question of my thesis work.

## 17.1. Will climate change and biological invasions act synergistically?

**“Even if a scientific model, like a car, has only a few years to run before it is discarded, it serves its purpose for getting from one place to another”**

**David Wingate**

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The widespread view that the main drivers of species extinctions will act synergistically<sup>24–27</sup>, and cause much higher numbers of extinctions than each factor individually, might be too pessimistic. Although the idea seems plausible that climate change could lift ‘thermal barriers’ for invasive species native to tropical or subtropical regions and thereby exacerbate problems caused by each driver individually, this has not been formally tested for an entire taxonomic group. The results of my studies suggest a more heterogeneous picture. Some invasive ants, such as the Asian needle ant, may indeed benefit from climate change and increase their suitable areas<sup>10</sup>. But others, such as the big-headed ant, decrease greatly at a global and regional levels in climatically favourable landmass<sup>13</sup>. Overall, invasive ants did not display a universal trend and in fact many species showed declines in suitable areas at a global and continental levels, suggesting that invasive species may not represent a ‘special’ group of organisms that would somehow systematically benefit from climate change while the rest of biodiversity is predicted to decline<sup>1,28,29</sup>. Similarly, the widespread idea that invasive species will simply “shift” to higher latitudes could not be confirmed in these studies. Both declines and increases of suitable areas could be observed at a wide range of different latitudes. Perhaps the ‘synergism dogma’ has become so widespread because conservation biologists tend to concentrate on potential threats to biodiversity and imagine ways in which species can go extinct and how threats could not only add up, but also act synergistically. With these concerns in mind, they may neglect the other side of the argument (but see<sup>30</sup>) and refrain from thinking about reasons why biodiversity may be *less* threatened than thought. In the context of my thesis, most published literature concentrates on a supposed increase of invasive species. But similarly, studies on the impacts of climate change do not generally stress the possibility that some species could *benefit* from climate change, although this has been suggested. For example, insects at higher latitudes might approach a thermal optimum if temperatures rise<sup>31</sup>. One reason for the lack of publications on that is obviously that non-threats do not represent a conservation priority. Additionally, ecologists may fear that writing about both positive and negative impacts of climate change on biodiversity or invasive species could result in ‘downplaying’ the risk of a mass extinction event caused (directly and indirectly) by humans. This, they may argue, would provide arguments for policy makers not to invest many resources in the protection of global biodiversity. I think that a simplistic picture

of 'all species are threatened by climate change' or 'invasive species will systematically benefit from climate change and invade higher latitudes' is not necessary and it might be more convincing to discuss the variety of possible responses and how resources could be best allocated to species at risk. In the case of climate change impacts on invasive species this more nuanced discussion is, however, difficult due to the lack of global taxon-wide studies. One recent study forecasted future ranges of the '100 of the worst invasive species' listed by the IUCN<sup>32</sup>, which is a very heterogeneous sample of invasive organisms that comprises microorganisms as well as plants, fungi or mammals<sup>33</sup>. Although these organisms are more difficult to compare with each other than a more homogeneous sample of invasive ants that I used as a model system, the important result of this study is the heterogeneity of responses, which supports my conclusions about the lack of synergism between climate change and invasive species. However, it should be kept in mind that both this study and the studies included in the present thesis use one particular class of model, species distribution models<sup>34</sup>. Although these are now widely used<sup>35-47</sup> and it is generally accepted that they can yield useful approximations about the future of biodiversity<sup>48-50</sup>, it should be underlined that they forecast a particular metric – the size of 'potential' ranges. Whether or not a climatically 'suitable' area will be occupied by an invasive species in the future is contingent on many factors, including the opportunity to colonize that area<sup>51</sup>. Even under current climatic conditions, 'potential' ranges are greater than realized distributions. Therefore, it may well be possible that a species for which I predicted a contraction in suitable areas (like the big-headed ant) would still expand within the suitable –still unoccupied-areas. As a result, it is possible that we will still see invasive ants expanding even if their 'potential' range has actually contracted<sup>13</sup>. If an increase in ant invasions were observed in the future, it would give support to advocates of the 'synergism' hypothesis. The problem is that the observable results of filling a 'potential' range and an expansion due to climate change increasing a potential range would not be distinguishable. It may be argued that this is, however, rather a limitation of the observational approach that is unable to discriminate between those two hypotheses. On the other hand, the model-based approach suffers from the fact that it only analyses the future trend in range size of invasive species – which is strictly speaking not a test of the 'synergism' dogma because the notion of ecological impacts is central to the way in which this idea has been put forward<sup>24</sup>. Climate change and biological invasions are both threats to biodiversity but their combined threat may be greater than the sum of both. Yet, species distribution models do not include any projected impacts. The underlying idea is that if an invasive species has a greater distribution in the future, its overall impact on biodiversity will be greater. This ignores the fact that climate change may affect the impacts of an invasive species without modifying its distribution<sup>34</sup>. For instance, if climate change has its projected negative impacts on native biodiversity, including local species loss, phenological asynchronisms among interacting species and disruption of mutualisms<sup>1</sup>, this will result in a certain degree of disturbance and weaken the community's resilience<sup>52</sup>. Thereby, climate change may increase the invasibility of a native community<sup>53</sup>. In that way, the increase in species' displacements could result from a 'synergy' between climate change and species invasions without any distributional shifts of the invasive species. This mechanism is, however, rarely discussed and evaluating a community's responses to climate change is rarely attempted<sup>54-56</sup> – and has, to my knowledge, never been coupled with the projected impacts of an invasive species. An additional difficulty is that even if an extinction event can be linked to a climate-change mediated invasion, this does not necessarily signify a 'synergistic' effect. If both threats

alone were sufficient to lead to the extinction of a species, it does not matter if one reinforces the other. For example, if an invasive ant threatens the native community on an island and climate change increases its impacts leading to extinctions, this may be called a synergistic effect. However, climate change itself might have been enough to lead to local extinction because the native species are trapped on the island without any possibility of migrating. The attribution of extinctions to synergistic effects is not straightforward and co-founding factors can obscure the picture. My studies are a first step to investigating the potential effects of climate change on suitable areas of invasive species. Although the results cannot refute the 'synergism' idea, they yielded surprising results and contradict the idea that invasive species will generally spread more with climate change and shift to higher latitudes<sup>25,57,58</sup>. In the future, it would be interesting to develop a new generation of models that take into account data on the species' genetics and demography<sup>59,60</sup>.

## 17.2. Which invasive ant species will dominate?

*"We must never make experiments to confirm our ideas, but simply to control them".*

*Claude Bernard*<sup>61</sup>

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As species distribution models only identify suitable abiotic conditions but do not take into account species interactions<sup>62,63</sup>, I carried out laboratory experiments confronting different highly invasive ant species. The underlying idea was that invasive ants encounter relatively little biotic resistance by native species during the invasion process; their spread is mostly determined by abiotic conditions<sup>64</sup>. However, different highly invasive species are known to exclude most native ant species and are therefore unlikely to co-exist in areas<sup>8</sup> that present suitable conditions for more than one invasive ant species. These potential 'invasion hotspots' have been mapped (Chapter 8) and the models have been identified species with potentially overlapping distributions. Using confrontation experiments at the individual, group and colony level over the short (5 min) to longer term (6 weeks), I explored dominance interactions among seven highly invasive ant species<sup>11</sup>. Although, I started the experiment with the idea in mind to identify *the* top invader, I would argue that there is no straightforward answer to the question which ant would dominate. Criticisms of the experimental approach include the lack of realism<sup>65-68</sup>. For example the ants had no brood to defend, colony sizes were kept relatively small (unrealistic for invasive species with millions of individuals)<sup>8</sup>, they were kept under artificial lab conditions, interactions were always conducted with symmetrical group sizes, the interaction space (petri dish or adjacent colony arenas) was constrained and made it difficult for the ants to avoid confrontations and the 'environmental' conditions (lab temperature and humidity) might favour one species over another<sup>69-71</sup>. But even though it may be preferable to study species interactions in the field, this is not possible in the case of invasive ants because currently there is no place on Earth where all these seven species exist in adjacent patches. Even in areas with two of the species, such as in New Caledonia where both *Wasmannia auropunctata* and *Pheidole megacephala* are present, interactions between the species are difficult to



study in field experiments because the species have a mosaic distribution (Hervé Jourdan, pers. comm). Some patches are dominated by one species, some patches by the other, with a 'no man's land' in between. Therefore, one would have to displace individuals of the two species anyway, in order to study the interactions – which would not be a 'natural' field experiment any longer. Within the laboratory settings that are stripped off the environmental complexities of the field, one can observe an increasing unpredictability of the interaction outcome with increasing complexity (and realism) of the experiment. In classical petri dish interactions with 1 vs 1 or 10 vs 10 workers, the outcome is fairly consistent and predictable (chapter 12). However, when colonies of 300 workers, which defend a queen, brood and a nesting space, are confronted, the outcome was much more variable (chapter 13). With the exception of *P. megacephala*, which went extinct in all replicates, all other species 'won' and 'lost' at least one interaction out of five replicates. The demographic processes that took place in different interacting colony pairs were very variable, as was the time to extinction of one of the contestants. When another layer of complexity was added and the simultaneous interaction of four species was tested, the results became unpredictable, and in two out of four replicated the least dominant species *P. megacephala* won, which normally invariably went extinct in colony confrontations. Because the multi-species experiment was time-consuming and did not yield any consistent results, I had to stop it after only four replicates and it is obviously possible that statistically significant patterns emerge after a great number of replicates. However, I would argue that the main point of this experiment is to show that increasing the complexity from a two species interaction to a four species interaction yielded unprecedented results, making the outcome unpredictable – at least based on the results of the dominance hierarchies constructed with petri dish interactions. This suggests that the outcome of interference competition in the field could be even more difficult to predict (if possible at all). In addition, I found a trade-off between the capacity of the species to dominate in confrontations and their capacity to discover and/or exploit resources (chapter 14). Such a 'dominance-discovery trade-off' has been discussed in the context of native ant communities and is thought to facilitate co-existence among species<sup>72-76</sup> (but see <sup>77</sup>). Consequently, it makes predictions about the different invasive ant species even more difficult. Co-existence among them is unlikely because they are all known for their highly detrimental impacts on native biodiversity and they are all individually capable of displacing many other ant species<sup>7-9,11</sup>. In addition, they have not been observed to exclude each other in the field. Perhaps there is no such a thing as a single top invader. Within the group of invasive ants, species excel at different capacities and have differing behavioural strategies. In a real field context, this may result in different species potentially being able to displace the other invasive species – depending on environmental conditions (perhaps predictable, but that would require the development of new modelling tools)<sup>70</sup>, and chance (inherently unpredictable).

But if one does not feel comfortable using a dominance hierarchy constructed under lab conditions to extrapolate to a real field situation, why conduct such an experiment in the first place? There are two answers to the question. The first, easy answer is that I did not expect these results and had imagined a more consistent, predictable outcome that would hold true when the level of interaction is the whole colony or a multi-species competition and I believe that the results which are much richer and more complex than thought are interesting in their own right. The second answer is that I think that it does not matter that much if the exact dominance hierarchy that I found in the controlled lab experiments is exactly 'true'. Of course, if one aims to get a directly applicable result that

can be used to inform management decisions<sup>78</sup>, one might be slightly disappointed with the results from these studies. I would rather argue – in line with the citation of Claude Bernard at the start of this paragraph<sup>61</sup> – that “one must never make experiments to confirm our ideas, but simply to control them” and that the main point of the experimental approach is to provide a controlled framework that allows to explore and discover new concepts and to develop ideas. The objective is more to be able to think about new concepts and to ask new questions than to create a pile of facts. Here, the three experimental studies that I conducted have allowed discussing several ideas, which –to my knowledge- have not been discussed in this form in the literature before and I think that some could open new research questions. Several key points of the studies are 1/ although invasive ants are an ecological homogeneous group they differ in their competitive capacities, 2/ there are two distinct behavioural strategies among invasive ants (evasive and aggressive), 3/ a single dominance index does not well represent the competitive relationships among the ants, 4/ increasing group size makes the outcome of symmetrical competition less predictable, 5/ different demographic patterns can emerge even though the initial conditions were the same in a controlled (and ecologically unrealistic) lab environment and 6/ there is a discovery-dominance trade-off among invasive ants – which are generally supposed to break this trade-off when invading native communities<sup>79</sup>. I believe that the most interesting part of these findings is not the much the exact result in itself, *i.e.* the *exact* order in the two-axis dominance hierarchy, for example, but mainly the discussion that follows; in this case why a commonly used single axis dominance index would completely misrepresent the competitive relationships among these species. The results of my experimental studies allow asking new questions. For example do the two distinct types of behaviour exist only when invasive ants are confronted with each other? Or do they exist when they are confronted with native ants, too? If some species display ‘evasive’ behaviour in the field, the general idea of the ‘aggressive’ displacement might not be true for all species. Perhaps the ‘evasive’ group uses a different mechanism to displace native species. Alternatively, they may be able to recognize a stronger interference competitor and adapt their behaviour accordingly, which would again be interesting. One might wonder how they could achieve that and if previous exposure to the opponent species plays a role in determining their behaviour. Similarly, one might ask whether single-axis dominance indices<sup>73,80–82</sup> represent well dominance relationships among native ants or how the predictability of competitive outcomes depends on group size (in native or invasive species). Perhaps there is a threshold number of individuals above which the outcome of an interaction becomes inherently unpredictable because the type process changes. Furthermore, it is intriguing to investigate further the processes that lead to different demographic patterns of colonies of equal size in my experiments. For example, do colonies of the same species differ in their behaviour<sup>83</sup>? In addition, it is interesting to know how strong native and invasive populations of a species differ. Apart from raising more research questions, the results may also have an applicable aspect for ant eradication<sup>78</sup>. It is usually thought that poisonous baits will not have excessively negative impacts on non-target species because the invasive ants excel at both discovering and dominating the resources. However, in the case of species like *W. auropunctata*, which is a rather slow discoverer, many faster discovering species could be harmed<sup>84</sup>.

Despite its limitations, the strong advantage of the experimental approach is that it allows investigating finer details of ant behaviour in a controlled environment, thereby helping to elucidate the mechanisms of invasiveness. Lab experiments can contribute to

gain a better understanding of the differences among invasive ant species in way that a field-based approach does not. The great majority of evidence of the impacts of invasive ants comes from correlational studies that document the presence of an invader and the simultaneous absence of many native species in the invaded area<sup>8,9</sup>. More rarely, manipulative experiments are conducted in the field, for example modifying the abiotic conditions or disturbance regime and recording the presence/absence of invasive and native ant species<sup>85-88</sup>. But these studies do not give insights into the mechanism by which invasive ants dominate. An exception is a study of the invasion of Argentine ants in a community of native ants in California<sup>79</sup> that demonstrated that Argentine ants are able to break the discovery-dominance trade-off in this community. This study is widely known because it gives an explanation for the mechanism of invasiveness. However, it only concerns a single species in a single locality and I think that more comparative studies of invasive ants are needed.

### 17.3. Is it possible to predict 'emergent' invaders

The literature on invasive ants has highlighted a certain number of ecological traits that are often associated with the so-called 'invasive syndrome'<sup>7-9</sup>. However, there are very few quantitative studies that compare traits in invasive ant native ants<sup>89,90</sup>. To my knowledge, there is no study describing an invasive 'profile' in a quantitative way. However, this could be extremely useful, especially if used for predicting future potential invasive species<sup>78</sup>. Surveillance efforts at ports of entry could prioritize species that are more likely to become invasive. Here, I have described a database (Antprofiler)<sup>23</sup> that I have set-up to study the traits in invasive ants compared to native or exotic ants. For many of the traits, there is currently not even an estimation of the general frequency in ants (e.g. polygyny). I have chosen 23 ecological traits and over two years of this thesis I have collected data on 2193 species from 166 genera and 21 subfamilies, a sample which does not seem to be strongly phylogenetically biased<sup>91</sup>. A preliminary analysis with 55 species was done for which I had sufficient data. The multivariate analyses showed a strong pattern – and were able to discriminate well between the groups of invasive and native ants, with the exotic species in between. Some exotic species fell rather in the group of the invasive species, suggesting that they are ecologically most similar and may be good candidates for becoming invasive at a later stage. Further analyses will be done including the effect of phylogeny and probably excluding some data deficient traits (thereby increasing the number of species that can be included in the analyses). In addition, the dataset will be strategically filled to complete holes that would enable us to add more species to the analysis. Nonetheless, the strong signal in our preliminary analysis is encouraging and strongly suggests that invasive ants have a very particular 'profile', that is shared by some exotic species (but none of the native species). Therefore, it seems that 'emergent invaders' may be predictable. As a next step, we plan to build a predictive model of ant invasions based on the characteristics of species.

## 17.4. How can the different approaches be integrated?

I used different approaches to study the future of ant invasions. The different methods used (models, experiments, database) are complementary in that they explore different aspects of a central question. Which ant species will pose the greatest problems in the future? A part of the question concerns the potential of known problematic invaders to spread further and to increase their invasive range. I attempted to give an answer by modelling the suitability of climatic conditions, which are a necessary precondition to the establishment<sup>64</sup>. As a second step, I have explored competitive relationship among ants with potentially overlapping distributions to construct a dominance hierarchy among those ants. The connection between those two aspects of my thesis is one-directional, i.e. the modelling part provides a justification for carrying out confrontation experiments to explore biotic interactions among different ant species. However, the results of the experiments cannot be fed back to the model results. If there had been a clear single dominance hierarchy among invasive ants in all aspects of competition (as was hoped when starting this project), it might have been possible to conclude that more dominant species displace the others from areas that they could both invade. In that way, it would have been possible to create spatial models that explicitly take into account these biotic interactions, similar to models of positively interacting species (e.g. butterflies and their host plants<sup>92</sup>) but with a negative interaction link. However, the results of the experiments suggested more complex relations between species, which made the prediction of co-existence or displacements of one invasive ant by another very difficult. Both types of studies, on abiotic conditions and biotic interactions explore facets of the future of ant invasions but they look at very different scales. Bioclimatic models identify suitable conditions at a very large spatial scale and cannot reliably predict the presence of a species at a very local scale of a few kilometres. On the other hand, biotic interactions increase in importance at this very small scale<sup>64</sup> and may in turn be affected by microclimatic conditions<sup>70,80</sup>, which are not explored by the global models. To better integrate these aspects, it would be interesting to perform interaction experiments under varying climatic conditions and to test the species' microclimatic preferences. Further, the large-scale climatic projections might be coupled with more local processes by linking the model outputs with local spread models from potential points of entry within a suitable landscape. This may allow inferring a more localized risk of occurrence of a particular species. The third part of the thesis, the construction of a database to test the characteristics of invasive ants<sup>23</sup> is a still on-going project with the objective to identify 'new' potential invaders. The other two approaches (modelling and experiments) assume that there is a fixed list of problematic invasive ant species. Yet, it is known that the invasions that we currently witness are related to the economic conditions of the last century<sup>6</sup>. That means that there is a substantial time lag between the introduction of species and the moment when they actually become invasive. Therefore, it is very likely that some ant species have been introduced or are currently being introduced via increasing global trade and tourism, and will later become invasive. Examples of recent invaders are *Lasius neglectus*<sup>93-97</sup> and *Pachycondyla chinensis*<sup>70,98</sup>, which have only recently started to become problematic. The aim of the database analysis is to produce a predictive model to identify new potentially invasive species. This is a different, somewhat disconnected part from the rest of the thesis. However, ultimately the results of this predictive model could be combined with the other two approaches. If species can be identified that have a high probability of becoming

invasive later on, it is possible to model their potential range and make spatial predictions about localities with a high risk of presenting suitable conditions for these species. Similarly, aggression tests may be conducted and the species' exploration and exploitation capacities could be assessed.

## 17.5. Should bioclimatic models be used to inform management decisions?

*"Predictions can be very difficult - especially about the future."*

*Niels Bohr*

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As a major biodiversity crisis is looming<sup>28</sup> and many species might go extinct by the end of this century, rapid actions are required. Future decisions about the allocation of resources to different conservation actions are in great need of scientific expertise and of projections to evaluate different options<sup>19,99-102</sup>. In this context, scientists are increasingly advocating the use of species distribution models to inform policy<sup>16,34</sup>. Despite the fact that a great number of limitations of these models are generally recognized<sup>35,62,103</sup>, a wide-spread view is that they can still deliver useful approximations<sup>49,50</sup>. Examples of potential applications include projections for threatened species<sup>1</sup>, the re-design of protected areas under climate change<sup>102</sup>, the management of invasive species<sup>104</sup> or human-assisted translocation<sup>99</sup>. However, it is evident that projections on the future of biodiversity vary a lot according to the taxonomic group considered, the metric of biodiversity loss, the drivers of global change considered (only climate change or also land use changes) or the date in the future for which the projection has been made<sup>20</sup> (chapter 2). These different sources of variability generate a wide variety of different projections – one not inherently closer to the truth than another, but simply based on a different set of assumptions. The question is how should one deal with this variety of different forecasts? Should a model of a suitable range for a given species inform management decisions? In the literature, an enormous number of problems has been raised, ranging from the issue of the 'double extrapolation in space and in time'<sup>44,105</sup>, when forecasting the potential range of an invasive species under climate change, to the best metrics to validate a model, AUC, Kappa, TSS<sup>34</sup>... Despite that, proponents of the practical application of models continue to argue that 'all models are wrong' and that one should stop worrying too much about a 'wrong' forecast because 'it is still better than no forecast'. Actually, I worry rather a lot - especially when I am told not to worry and I find especially disturbing the sentence 'all models are wrong' that modellers like to say. Does wrong equal wrong? Or is there a 'little bit wrong'? Very wrong? Averagely wrong? A little bit more than a bit? Less than a lot? Fairly wrong? Or a little less than a lot but a fair bit more than averagely wrong? Or totally dead wrong? If one considers that the models are 'useful', then the implicit assumption is that they are wrong in that they do not accurately reflect reality but are better than a chance prediction and better than an expert opinion. All models reduce reality to a simplified equation with a certain number of variables that are thought to affect a given model output. In certain cases it is easy to recognize the utility of a model, which gives inaccurate but close-to-reality outputs and the model 'wrongness' is simply a degree of

imprecision in the calculation, which becomes irrelevant depending on the accuracy that is needed for a practical application. For example the framework and calculations using Newtonian physics are sufficient for most types of applications in daily life. However, if a greater degree of precision is needed, Einstein's relativity needs to be invoked, such as in the case of the GPS. So, Newtonian physics could qualify as 'a little bit wrong' but still an extremely useful approximation for most situations. Let's consider the case of species distribution models. Is wrongness here a matter of imprecision or a question of perhaps being deadly wrong? The question is not as straightforward to answer as in the case of a mechanical equation system. In order to generate the model output of a species distribution model, one has to make a *series* of hypotheses. First, one has to choose different human development scenarios of the future that generate different CO<sub>2</sub> emission scenarios<sup>4</sup>. This is already problematic, as it is completely uncertain what the world will be like by the end of the century in terms of political and economic organization and how many humans will populate the planet, how agricultural practices will change in the future and what scientific developments will have been made that could increase or decrease the emission of greenhouse gases. Second, to model how the climate will respond to different human development scenarios, one has to model the climate physics of the planet using large simulations (Global Circulation Models)<sup>4</sup>. There are more than 20 Global Circulation Models, each based on a different combination of physical assumptions. No single one can be said to be better than the others, as climate physics is extremely complicated and the system interactions are not well understood. Together, a given CO<sub>2</sub> scenario and a Global Circulation Model give a forecast for a specified year in the future – of different variables based on temperature or humidity. However, these outputs are at the scale of enormous cells (about 500 x 500 km) because the calculations are so heavy that it would take years for a computer to directly simulate the climate at smaller cells<sup>106</sup>. However, the climate at this scale is not relevant for most applications like species distribution models. Therefore, modellers use a 'trick'. They statistically 'downscale' these projections, using known relationships between large-scale and small-scale climatic variables<sup>107</sup>. Then, an ecologist selects a certain number of variables believed to be relevant in determining the distribution of a focal species. He (or she) then has to get distribution points of the species (thought to be representative of the species entire distribution and to reflect correctly its ideal climatic conditions)<sup>38,108</sup> and then select an algorithm<sup>34</sup> linking the distribution data to the climatic data. The 'final' model then is a description of the species current climatic niche that can be projected on different climatic scenarios of the future. This is the short version of the species distribution modelling process; of course there are many more steps that I haven't detailed here. The point is that the final output depends on a number of nested hypotheses and whether or not such an output can be useful seems questionable to me. I would divide the question into 'methodological issues' and 'conceptual issues'. The first group is related to problems that science will be able to answer in the future. For example, questions related to the ideal number of pseudo-absences<sup>109</sup> that should be used to model a species' distribution or the best metric to evaluate the performance of a model or the development of better performing algorithms<sup>34</sup> seem to be answerable. A vast number of studies are concerned with these rather technical questions and the body of scientific knowledge about these issues is starting to build up. Individual studies add building blocks to these methods and increasingly improve the predictive quality of these models. On the other hand, there are a certain number of 'conceptual' issues that are more difficult to deal with. This second category can be illustrated with two examples from my own studies. For instance, the

output of a species distribution model is not a binary projection of areas where the species is likely to be present or absent, but it is a probability of occurrence or a suitability index. For many applications however, a classification into 'suitable' and 'unsuitable' areas is needed<sup>110</sup>. For example, when a species' potential distribution is evaluated under current and future climatic conditions and the change is quantified. In the literature, there are many studies concerned with the selection of an optimal classification threshold<sup>110</sup> that can depend on the application of the species distribution model. However, in one of my studies (chapter 6) I pointed out that the act of selecting a classification threshold can be misleading in itself. In reality habitat does not fall into 'suitable' and 'unsuitable' categories but presents different degrees of suitability of a species. The relative suitability of abiotic conditions determines establishment likelihood in conjunction with other factors such as biotic interactions. In the case of an invasive species that I illustrated in chapter 6, the improvement of relative suitability can help the species overcome biotic resistance for example and ultimately lead to the establishment of the species. Therefore, it is very important not to lose the information about relative suitability of a pixel and quantify the changes in relative suitability in some way. I suggested one way to do that by calculating a suitability index. In this study, I showed that the binary classification via a selected classification threshold can lead to serious qualitative mistakes in the interpretation of the model output; i.e. the potential of *Myrmica rubra* to benefit from climate change via a qualitative increase of suitability would have been overlooked by a binary classification method. A second even more striking example of 'conceptual' issues of species distribution models comes from chapter 10. Here, I forecasted the potential distribution of 15 ant species under current climatic conditions and three future time horizons (2020, 2050, 2080) and observed 'trend reversals' in six out of 15 species, i.e. an initial range expansion was followed by a retraction or vice versa. In four species this 'trend reversal' even changed the sign of the prediction, i.e. depending on the time horizon in the future one would have predicted either an increase or a decrease in suitable areas. If a management decision were based on a projection to a single time horizon in the future, it could have potentially disastrous decisions. Even when the forecast is carried out for different dates in the future and a decision maker has knowledge about the possible trend reversal for a given species, it is far from clear how this knowledge could be used to optimize the management options. The fact that 6 out of 15 species in my sample displayed a trend reversal is rather worrying if the objective is to apply these models in conservation. I believe that these more 'conceptual' issues are at the heart of the question whether or not species distribution models should be applied. These two studies<sup>12,20</sup> illustrate how 'dead wrong' a decision based on a model can be. This type of 'wrongness' is qualitatively different from the 'wrong' models that still yield useful approximations. I believe that there is a danger that modellers do not discuss enough the possibility of being 'dead wrong'. This is perhaps explained by the fact that the modelling community needs to defend the approaches towards numerous critics within ecology and outside of it<sup>111</sup>. The temptation is great to downplay the seriousness of conceptual issues that have the potential to totally invalidate a model. The general attitude of researchers in the field seems quite defensive and papers concerned with problems of species distribution models are often providing already a solution. For example, studies showing the immense variability among forecasts based on different model inputs often describe methods to "deal" with that, such as consensus forecasting<sup>112</sup> or mapping spatially areas of greater or lesser uncertainty<sup>113,114</sup>. The main message in these studies is: yes, there is uncertainty but no, that is not a major problem – there are ways to deal with it<sup>115,116</sup>.

However, it might be interesting to read about the meaning of this large degree of uncertainty and potentially unsolvable problems. I believe that there must be many other serious conceptual issues with these types of models, which have not been described in the literature yet – given that I came across two of them in the short time span of this thesis. Therefore, I think that it is premature to advocate direct application of species distribution models in conservation<sup>16</sup>. I think that in many cases a decision based on a model is not better than a decision without the model. However, comparisons among many species may be useful to predict an overall response of biodiversity to climate change – if positive and negative errors are the same across species and finally average out. In that sense, predicting the location of potential invasion ‘hotspots’ for example in France (chapter 9) or worldwide (chapter 8) is certainly more reliable than the prediction of suitable areas for a single species (chapters 5 and 7).

## 17. 6. Is climate change predictable?

***“What a curious attitude scientists have ‘We still don’t know that; but it is knowable and it is only a matter of time before we get to know it’ As if that went without saying.”***

***Ludwig Wittgenstein<sup>61</sup>***

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When thinking about the reliability of species distribution models, one has to distinguish between predictions for current or future climatic conditions. This argument is rarely mentioned in the literature but it is important to note that predictions for current climatic conditions present a much lesser amount of uncertainty as they are based on present climatic conditions that have been *recorded*, instead of future projected climatic conditions. Nonetheless, even current recordings present certain limitations, such as the very unequal distribution of weather stations around the world that record temperature and humidity<sup>4</sup>; a factor that contributes to higher levels of uncertainty for sparsely covered regions (such as Africa). But an entirely different level of uncertainty is reached when climatic forecasts for the end of the century are made. In the previous paragraph, I have already touched upon the question of ‘nested’ hypotheses concerning CO<sub>2</sub> emissions and climate physics simulations<sup>34</sup>. In the case of CO<sub>2</sub> emissions, one might argue that it is not essential to entirely understand the functioning of society and policy options in order to develop scenarios of ‘reduced’, ‘similar’ or ‘increased’ greenhouse gas emissions and explore the impacts of each<sup>17</sup>. However, the case of global circulation models that simulate the climate physics is different, because it is not possible to build a finite number of scenarios with a likely truth somewhere around a central tendency. This is because the simulation of global climate requires *functional* understanding of a complex system. Although progress has been made in the field, even current global circulation models are far from representing even approximately the complexity of the Earth’ climate system<sup>18</sup>. Indeed, they mainly simulate the dynamics of the atmosphere and the oceans but many aspects remain neglected, such as the chemistry of the atmosphere, the carbon cycling in the biosphere and the interaction with small particles the stratosphere<sup>18</sup>. Models differ considerably in their projections of how different



components of the global climate systems will interact, particularly cloud feedbacks<sup>119-121</sup> and oceanic heat uptake<sup>122,123</sup>. Additionally it remains very unclear how aerosol emissions will influence the changes in temperature, precipitations and cloud formation<sup>4</sup>. Further, there is a great disparity in the confidence in projections for different climatic variables<sup>4</sup>. For example, models vary in their projections in regional increases in temperature (Fig 1). Despite the variations, a temperature rise for a given area can be said to be likely constrained by a lower and an upper limit. In this case, it seems reasonable to forecast potential future impacts based on these scenarios.

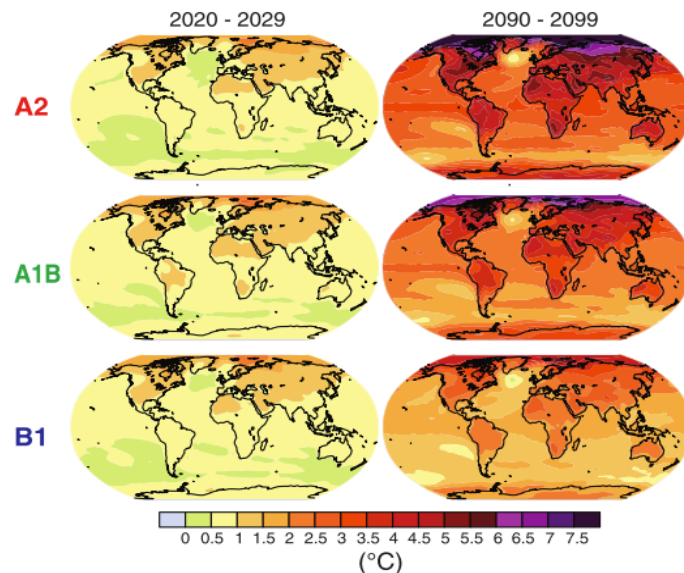
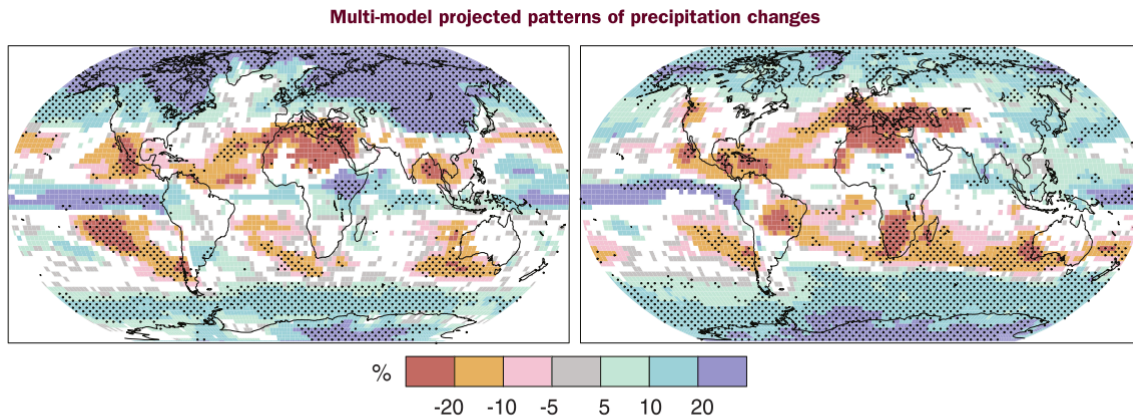


Fig. 1. Global increases in temperature

On the other hand, projections in precipitation changes are much more variable<sup>4</sup> (Fig 2). In the figure, large parts of terrestrial landmass on all continents are coloured in white, which signifies that less than 2/3 of the models agree in the *sign of change*. That means that the models are not even able to predict the *direction* of change in these areas, i.e. whether precipitations are likely to increase or to decrease. Given that precipitations are at least as important as changes in temperature for ecological systems, this casts a serious doubt upon the predictability of the future of biodiversity under climate change within these areas.



**Figure 3.3.** Relative changes in precipitation (in percent) for the period 2090-2099, relative to 1980-1999. Values are multi-model averages based on the SRES A1B scenario for December to February (left) and June to August (right). White areas are where less than 66% of the models agree in the sign of the change and stippled areas are where more than 90% of the models agree in the sign of the change. {WGI Figure 10.9, SPM}

Fig. 2

Another problem is the prediction of extreme events, which are rare. Extreme climatic events, such as droughts, floods, hurricanes, extreme rainfall or frost are predicted to change in frequency and amplitude with climate change<sup>124</sup>. The difficulty in understanding the factors that influence the occurrence of extreme events is the scarcity of reliable time series data<sup>118</sup>. Therefore, future climatic projections do not include these extreme events and the climatic variables that are usually used include only mean values (e.g. average temperature, mean temperature of the warmest quarter, mean precipitation of the wettest quarter). Even the variables that are supposed to represent the 'extremes' (warmest, coldest etc) are based on monthly or yearly averages and are not the same as the projection of an extreme event<sup>4,106</sup>. However, it might well be that these extreme events have a much greater influence on biodiversity than averaged variables<sup>124</sup>. For example, if the frequency of short heat waves increases, this could directly kill many species in the same way as the 2003 heat wave killed many older or fragile people in Europe<sup>125</sup>. Similarly, a small number of extremely cold days can suffice to hinder an invasive species from establishing in a given area because it directly kills the species. If the frequency and intensity of these extremely cold days decreases, it could allow the species to invade. This factor is totally overlooked in species distribution models based on variables provided by the IPCC Worldclim dataset<sup>4,106</sup>. Furthermore, many components of the global climate system can interact in unexpected ways, creating feed-back cycles that could reinforce impacts of climate change<sup>118</sup>. In this context, so-called tipping points are especially worrying<sup>126-128</sup>. Climate change leads to non-linear processes with 'bifurcation' points where the whole system changes from one state to another state, when a systemic threshold is exceeded. The crossing of these thresholds can lead to a system switch, *i.e.* a small change can lead to a large-scale change in the global climate system. Once these tipping points are reached, the system has crossed a point of no return. The existence of these planetary tipping points has been debated and some can be imagined but they are extremely difficult to predict<sup>127</sup>. One such potential tipping point concerns the breakdown of the thermohaline circulation (THC), which brings warm tropical water into the North Atlantic and warms in this way Northern and Western Europe by several degrees Celsius<sup>128</sup> (Fig 3). In addition, it increases precipitations in the whole region.

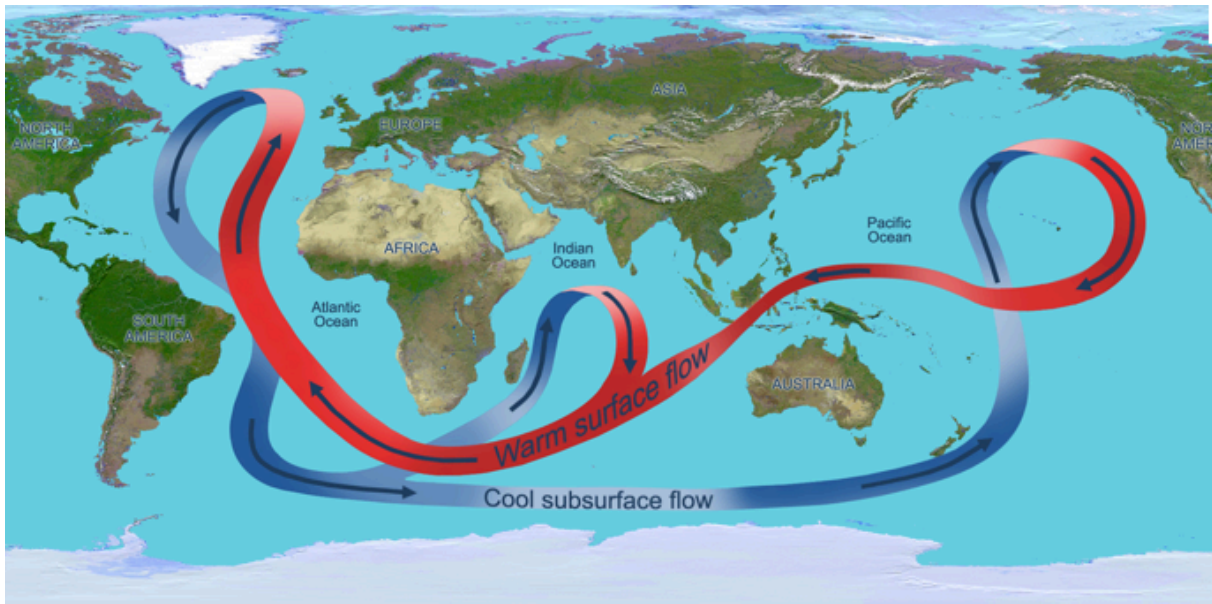


Fig. 3 Thermohaline circulation. Image credit: NASA

Models and paleoclimatic data have shown that several equilibrium points for the THC exist and rising temperatures could shift the equilibrium to another stable point. In particular the Gulf Stream could slow down or even stop<sup>128</sup>, which would have enormous consequences for marine ecosystems and the ocean's capacity to absorb CO<sub>2</sub>. Another potential tipping point is the capacity of the ocean and biosphere to absorb CO<sub>2</sub>. In fact, it has been suggested that climate change could even lead to a net release of greenhouse gases by the biosphere, leading to a positive feed-back loop<sup>128</sup>. Further, the melting of the large ice sheets (Western Antartis, Greenland) could be a tipping point but the threshold for this event is equally difficult to predict<sup>126</sup>. In addition, it has been suggested that not only the climate system but also the responses of the biosphere to climate change exhibit tipping points<sup>129</sup>. Overall, predicting future climate change is much more complex than just creating scenarios of temperature rise between 2°C and 4°C for example. As long as climate physics has still many interactions and feed-backs to explore<sup>118</sup>, it is difficult to make ecological predictions. Yet, I believe that this should not stop ecologists from attempting to forecast different responses of biodiversity to climate change, because ideas and concepts can evolve within this framework. Models can serve as a basis for discussion about the future of biodiversity. However, when concrete results are discussed, they should be viewed in the light of the assumptions imposed by the numerous inherent complexities of atmospheric physics and projections of ecological systems.

## 17.7. Do consensus models solve the problem with uncertainty in species distribution models?

*“Man has an intense desire for assured knowledge”*

*Albert Einstein*<sup>61</sup>

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Any model prediction is based on a particular set of assumptions and scenarios, but no single bioclimatic model is inherently better than another one. They simply represent different possible future scenarios. The question that arises is what to do with this variety of different projections. How can one synthetically present the information content of these multiple projections? Probably the most honest way to deal with the question would be to simply present all model outputs side by side. However, this makes it difficult for the eye to spot a pattern and additionally some kind of summary is often required. Even scientists have a desire for assured knowledge and generally prefer showing a synthetic map of ‘the most likely’ future instead of showing 30 maps that reveal how very different individual forecasts can be – in the latter case anybody looking at these maps would immediately ask if there is anything useful about the information content in these forecasts. In some way, a consensus model occludes that variability or, alternatively, one could say that it ‘takes into account’ the variability<sup>112</sup>. I have used consensus models for practical reasons (it is not easy to present 90 maps for each of the 15 species) and because they are following the current ‘best practice’ standards in the field<sup>34</sup>. The underlying reasoning is that any particular model is considered to be ‘false’ but that a multitude of models can help to separate a ‘signal’ from the noise<sup>112</sup>. Therefore, a consensus model is considered to be better than any particular single model. In principle, this idea could be true if different model outputs represented a range of scenarios – for example the suitable range of a species when the temperature rises by 2, 3, 4 or 5 °C. Yet, as I have discussed earlier, climate change is a much more complex phenomenon and atmospheric physics still lacks fundamental knowledge about the functioning of the system and internal feed-backs<sup>4,118,128</sup>. Therefore, it is entirely possible that any single model or subset of models is much more closer to the ‘truth’ than the others. In addition, the relevance of

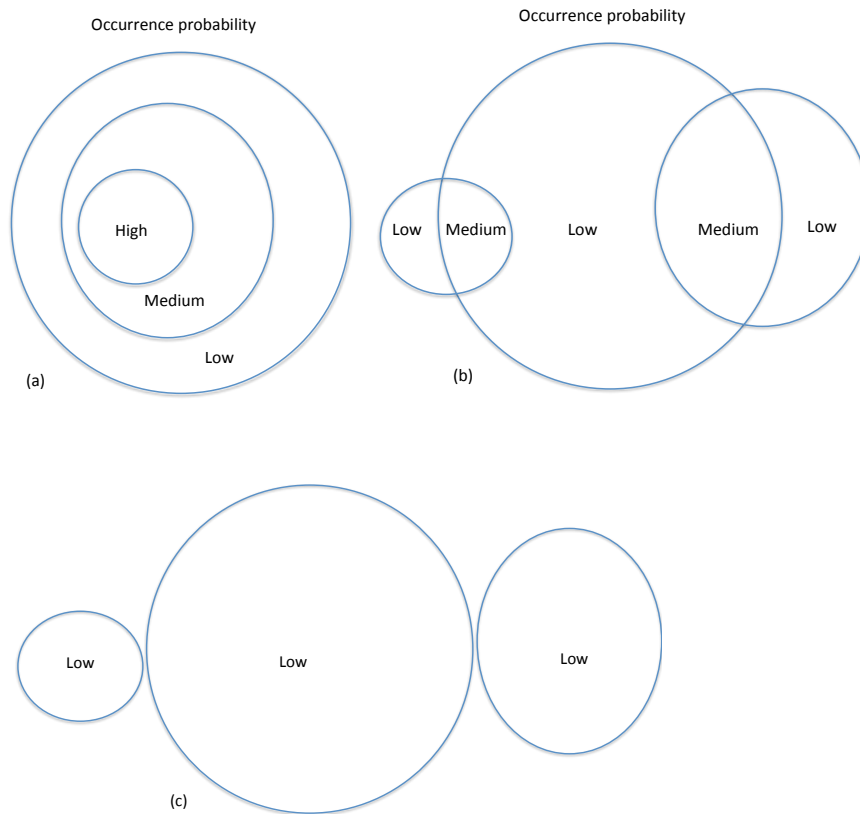


Fig. 4 Spatial predictions of three individual models based on different possible future climatic scenarios. No single model is supposed to be inherently better than the other; they represent different possible processes. A consensus is generated by superposing the projected ranges of the individual models. Areas where two or three models predict a presence of a species are deemed to be more favourable than areas where a single model predicts potential habitat.

consensus models depends on the spatial arrangement of the individual model outputs (Fig 4). Let's consider the first case (Fig 4a) where three individual models essentially represent the same future scenario. They are totally overlapping; only they predict a suitable range of a different size. In this case, a consensus model seems to be a reasonable option to synthesize the three results. The smallest, central area is predicted by all three models and therefore the modeller can have high confidence in the projection. This area totally coincides with the projection of the most restrictive model of the three. If we consider the second scenario (Fig 4b), we can see that there is no area where all three projections agree. Areas where at least two agree are deemed 'more suitable' than areas where only a single model predicts suitable conditions. These two areas are however spatially disconnected. If one applies a classification threshold that considers all 'low' areas as 'unsuitable' and all 'high' or 'medium' areas as 'suitable, one would obtain a prediction of two separated patches. A potential user of this model could interpret this as the existence of patchily distributed suitable habitat, for example related to some climatic variable that is necessary and is only favourable in these two patches. However, as we have seen, the existence of the two patches can be entirely due to an artefact because the three models represent different processes. It is possible that there is nothing patchy about the distribution of climatic conditions in the study area and that the three model outputs lie on a continuum of climatic conditions and simply present three different hypotheses. In this case, it would be rather unlikely that *both*

'medium' patches present suitable conditions and not the area in between. In that case, it is already less obvious to decide if the consensus method is adequate. There is no way (yet?) how the model user could trace back the spatial output to the individual models and relate that with the distribution of climatic conditions and the hypotheses that have been made concerning the climate and the relationship between the climate and the species distribution. The consensus model summarizes a lot of complex information that might not be directly interpretable<sup>34,112</sup> but at the same time it may omit essential details about the spatial arrangement of individual models for example. In the third case (Fig 4c), the consensus model is clearly inadequate. Here, one would conclude that the entire study area does not present suitable conditions for the species (or only very low suitability conditions). Yet, the uncertainty in the climate projections is such that there is no overlap among individual models. However, all individual projections have predicted a certain amount of suitable landmass – but in very different localities. It is not obvious how this result should be interpreted. I would argue that in this particular case, it might be better to present a mean value across all projections, representing the mean size of the suitable area (instead of the value of the consensus model). However, no reliable statement can be made concerning the location of this suitable area within the study area, *i.e.* no map of suitable conditions can be provided that corresponds to the mean estimate. For the moment, consensus models remain the best available method to forecast species distributions, given the variability among different forecasts. But they have their own pitfalls and future research could also aim to develop better methods to summarize variation among model outputs in size and in their spatial location simultaneously.

## 17.8. Can the models be verified?

*“One of the most insidious and nefarious properties of scientific models is their tendency to take over, and sometimes supplant, reality”*

*Erwin Chargaff<sup>61</sup>*

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How can one choose between different models representing possible versions of reality? Is there a way to verify a model? Can one prove a model? The answer to that is clearly no because the word 'proof' should refer exclusively to deductive reasoning<sup>130</sup>. Most scientific theories do not fall into that category<sup>130</sup>. But how can one decide if a theory or hypothesis is 'scientific' if it is not possible to prove it? Karl Popper has proposed a criterion of demarcation that distinguishes science from non-science: falsifiability<sup>131,132</sup>. According to his theory, no scientific law or hypothesis can ever be proved, it can at best, be given a high degree of probability but there must always remain the possibility that a piece of evidence will one day be found to prove it wrong<sup>133</sup>. For example, let's consider the following: "All Germans like beer. Cleo is German". If both statements are true, it must follow that Cleo likes beer. We know that she is German, so we could test the hypothesis about Germans. However, if we ask her and she answers that she likes beer, that doesn't prove the hypothesis. On the other hand, if she says that she doesn't like beer, then we have falsified the statement 'All Germans like beer'. The goal of science is to produce statements, which are high in information content and low in the probability of being true (since the more information contained, the greater the chance of finding a proposition to be false), but which actually come close to the truth<sup>133</sup>. It is easy to

produce statements that will never be refuted (e.g. the sun will rise tomorrow, the sky is blue during the day, all French like baguette, wine and cheese...) but they contain so little information content that they will not be of much use<sup>133</sup>. Species distribution models are high in their information content as they make spatially explicit predictions for many pixels on a map and it seems obvious that this very explicit and rich information leads to a high probability of the models being wrong. But are they falsifiable? How could one refute a species distribution model? There are two ways in which a species distribution model could make a wrong prediction for a given area. Either the model predicted a presence in the future and the species is found to be absent or the model predicted an absence and the species is found to be present. Would these mistakes be considered to falsify the model? I think that in the first case (predicted presence, actual absence), the answer is no. There are many reasons why a species would not be present in a place that really does present suitable climatic conditions as predicted by the model. For example, it might be due to a lack of opportunity<sup>51</sup>. Perhaps the species has not been introduced to this area or it has but is very slow to spread and has not been detected<sup>78,134</sup>. Another possibility is that biotic resistance does not allow the species to establish. In addition, there may be other limiting factors (resources<sup>135</sup>, nesting spaces<sup>135</sup>, biotic interactions<sup>46,136</sup> that were not considered in the model) that might be responsible for the species' absence. Overall, if a species is absent in an area where it was predicted to be present, this does not invalidate the model. In the second case (predicted absence, actual presence), there are also a multitude of reasons at hand that could explain this prediction error, without invoking a faulty model. Perhaps the observed presence is not of a permanent nature<sup>137,138</sup>; the climate is not favourable for the species but it managed to survive for some time in the area. In that case the extinction of the population is a matter of time<sup>139</sup>. Similarly, it could be that the species established during a favourable period of the year (e.g. warm summer month) but that the climate at another moment (e.g. colder winter month) will later kill the population. Or, the species is associated with human-modified climatic conditions; this could be especially the case for ants that can invade houses or agricultural areas and do not experience modified climatic conditions<sup>7,8,88</sup>. Another possibility is that a niche shift occurred and that the species evolved a tolerance to different environmental conditions<sup>44,103,140</sup>, which would not falsify the model either because the model only makes a statement about the species current climatic niche. It could also be that the species' fundamental niche is much larger than its realized niche<sup>141</sup>, which has been estimated, based on occurrence points. In that case, no evolution is required for the species to establish under climatically different conditions than in its native range. In that case, the prediction 'error' is not a fault of the model either, which might have correctly associated the environmental variables with the occurrence data to describe the species' realized niche. Overall, it seems to me that a species distribution model is neither testable nor falsifiable. In that, it does not fit Popper's demarcation criterion<sup>131,132</sup> that he used to define 'science'. However, Popper's view of the scientific theories that are rejected if they are falsified by a piece of evidence has been heavily criticized. For example, Thomas Kuhn argued that science does not proceed in this way in reality<sup>130,142</sup>. When a fact is found to be incoherent with the theory, it usually does not lead to a rejection of the theory but of the fact, or an extension of the theory to accommodate that piece of evidence. Therefore, falsification is practically irrelevant<sup>130</sup>. Yet, I believe that the case of species distribution models does not entirely fit with Kuhn's argument either. Kuhn considers the case that a contradicting fact is found which does not lead to the rejection of the theory<sup>142</sup>. In so far, this would be the case for a

prediction error in a species distribution model that would not lead to the conclusion that the model has wrongly described the species' climatic niche. However, there is an important difference. In Kuhn's view, the decision of whether or not a contradicting piece of evidence leads to the refutation of the theory is made *a posteriori*, that is, once the problematic fact has been discovered. In the case of species distribution models on the other hand, a modeller has already a set of (published) *a priori* reasons not to reject the model – even if contradicting evidence is found later. A further complication is that species distribution do not just predict an 'event' or 'non-event' but in fact a probability of occurrence in a certain place<sup>34</sup> and it is not clear how a probability of a single event could be falsified. One could say that, consequently, modellers lead a comfortable and 'safe' life – whatever the future will bring, it will not lead to a fundamental rejection of their work. This might be considered to be conceptually problematic. But perhaps, we should not try to view research in the light of the restrictive demarcation criterion? Maybe it is not possible to find a universal definition of scientific research that demarks it from pseudoscience? The philosopher Ludwig Wittgenstein has argued that there is no fixed set of features that define a 'game'. Rather there is a loose cluster of features most of which are possessed by most games<sup>130</sup>. But any particular game may lack any of the features in the cluster and still be a game. The same may be true for science<sup>130</sup>.

## 17.9 Is it the aim of models to predict the truth?

*"As far as the laws of mathematics refer to reality, they are not certain; and as far as they are certain, they do not refer to reality"*

*Albert Einstein*<sup>61</sup>

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At a first glance, the question whether or not models aim to predict the truth seems silly. Even if models do not predict the truth, they should at least *aim* at predicting the truth, to get as close to the truth as possible. But what is the 'truth'? Generally, we mean by the truth something that accurately and objectively represents the reality, something that we could call a 'fact'. But it should be noted that all the terms used in the previous sentence ("accuracy", "objectivity", "reality", "fact") are quite vague and have more than one definition<sup>143</sup>. Some might argue that a 'reality' or a 'fact' should have at least a precise meaning when they are used in a scientific context. But it has been argued that collected data are invariably constrained by theoretical assumptions and that it would be impossible to get a set of 'pure' data that all scientists would accept irrespective of their theoretical persuasion<sup>130</sup>. This is being referred to as the "theory-ladenness of data"<sup>142</sup>. Further, any piece of evidence is collected using scientific instruments and protocols and our sensory perception is used to 'record' the data<sup>130,133,143</sup>. Moreover, this data is always interpreted by the researcher within a 'paradigm', according to Kuhn. A paradigm consists of two main components: firstly a set of fundamental assumptions that all members of a given scientific community accept at a given time; secondly a set of problems that have been solved by means of those theoretical assumptions and that appear in the textbooks of the discipline<sup>130</sup>. In that, niche theory as a set of fundamental assumptions and species distribution models as a set of problems, could fully qualify as a paradigm. When scientists agree on a paradigm they share a whole framework of conceptions and an outlook on how progress in their field can proceed<sup>142</sup>. Normally, the objective is not to test the paradigm itself but to conduct the research within the



paradigm. Eventually, if more and more contradicting pieces of evidence accumulate, the paradigm is replaced by a new paradigm that accommodates these observations. Any fact is always seen within a single paradigm<sup>131</sup>. For example the concept of “mass” has a different meaning in classical mechanics or in Einstein’s relativity. This exclusivity of ‘world views’ has been called incommensurability<sup>144</sup> and is analogous to the observation of an optical illusion (Fig. 5), where one cannot see at the same time the two batmen or the wolverine face in the middle. One has to choose between two perspectives.



Fig. 5 Optical illusion, depending on the perspective. One wolverine or two batmen?

Kuhn argues that if any fact has to be seen as a part of a paradigm, the concept of an ‘objective truth’ has to be questioned<sup>130</sup>. In the case of niche theory and species distribution models, most studies are concerned with either applications of the concept (e.g. predictions of potential ranges for invasive species, chapters 5-10) or with technical advances in the field of species distribution modelling. Both can be scientifically evaluated within the theoretical framework (or paradigm) underlying the application of species distribution models. In that sense, it is indeed the objective of the models to predict the ‘truth’ – but a truth, which is confined within this framework<sup>130,133,144</sup>. However, according to Kuhn it is not possible to make a general statement about the relation to ‘reality’ of the whole framework. Maybe the main focus should not be to know whether or not the framework reflects truth or whether it is falsifiable but rather whether or not it can be useful. Unfortunately, the main interest of the field lays in future predictions and therefore, there cannot be any estimation of the usefulness of species distribution models with climate change so far. Strict definitions of ‘facts’, ‘truth’ or ‘science’ may be theoretically interesting but practically irrelevant. As Paul Feyerabend puts it “It is clear that the idea of a fixed method, or of a fixed theory of rationality, rests on too naive a view of man and his social surroundings. People are craving for intellectual security in the form of clarity, precision, ‘objectivity’ and

'truth'"<sup>145</sup>. He argues that any kind of argument or hypothesis will make science progress and should not be excluded. Science mainly advances through debate and the confrontation of ideas and even opposing or unscientific concepts can help because they force the opponents of a theory to reinforce their arguments<sup>145</sup>. Personally, I like the view of Feyerabend because I believe that the main purpose of species distribution models is to provide a theoretical framework, which can be used to develop ideas, concepts and a general debate – all of which are independent of a concrete projection.

## 17.10. Conclusion

*"Science says the first word on everything and the last word on nothing"*

*Victor Hugo*<sup>61</sup>

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I used three different approaches to predict future ant invasions: species distribution modelling, laboratory experiments and a database analysis. All of these approaches have their particular limitations and merits. Especially species distribution models are based on a series of underlying assumptions and the uncertainties are great concerning their usefulness in predicting future ranges of invasive species under climate change<sup>34,62,63,140</sup>. I believe that these models should mainly be used as tools to develop new ideas and concepts and one should be careful in taking them literally as a representation of reality. The current claim to move on and start applying these models in conservation<sup>16</sup> leads to a risk of over-interpreting the results. In principle, it might be preferable to have a model estimation rather than not when making a decision, but the great conceptual and technical problems associated with this approach should be kept in mind. Generally, decision makers will have other arguments to decide among different conservation options and these other arguments may be scientifically sounder – although a beautiful map can be very convincing. For me, the most important aspects of my work are not the concrete predictions themselves but rather the use of different tools to discuss more general themes in global ecology: the 'invasion-climate change synergism'<sup>24,25,57</sup> (Chapter 8), invasion hotspots (Chapter 8), quantity vs quality of suitable habitat (Chapter 6), trend reversals (Chapter 10), different behavioural strategies in the invasion process (Chapter 12 and 13), trade-offs in different aspects of ecological dominance (Chapter 14), trait-based predictions (Chapter 16)...

For me, both models and experiments are tools to test and express ideas. The main objective is to add new points of view to the general discussion, not to take the results literally. Nonetheless, I think that some more concrete conclusions can be made, too, concerning the future of ant invasions. Overall, invasive ants do not seem to increase their potential range following climate change. Instead, they are predicted to follow rather the trend of biodiversity in general<sup>1</sup>, i.e. many species might decrease their suitable range in the future. Comparing multiple models of multiple species of invasive ants, potential invasion hotspots can be identified, which seem robust to the use of different methods and climate scenarios. These invasion hotspots coincide largely with the biodiversity hotspots – the most species rich and vulnerable regions in the world (Chapter 8). This suggests that ant invasions are likely to remain a major problem in the future (Chapter 8). Although, I would be careful with a too detailed interpretation of single species forecasts, I think that some conclusions can be drawn from species or area

comparisons and relative risk assessments may be meaningful, such as the assessment that I have carried out for French departments and main ports of entry (Chapter 9).

Species interactions are more difficult to predict based on the results of the experiments owing to several facts: there seem to be two different behavioural strategies (evasive and aggressive) and it is unclear how those groups would interact in the field and if they could co-exist (Chapter 12). Second, increasing complexity from single worker to whole colony interactions shows that the processes become less and less predictable and the environmental conditions may also play a large role in determining which species will dominate (Chapter 13). In addition, I found a trade-off among four invasive ant species between the capacity to explore or exploit the resources and their capacity to dominate them (discovery-dominance trade-off) (Chapter 14). As this trade-off is supposed to favour co-existence in native communities, it is an open question what this result means for the interaction between these invasive ant species in the field. It suggests a potential co-existence, but this is not coherent with previous observations at invasion fronts.

In summary, this thesis has opened more new questions than it answered but these questions are a result of the work that I conducted and even more interesting than the accumulation of a pile of facts.

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## Monster fern makes IUCN invader list

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# Correspondence

## Monster fern makes IUCN invader list

The list of 100 of the world's worst invasive alien species, compiled by the International Union for Conservation of Nature (IUCN), aims to help biodiversity conservation efforts worldwide (see [go.nature.com/qa9z1g](http://go.nature.com/qa9z1g)). After a position on the list fell vacant as a result of the global eradication of the rinderpest virus (see, for example, *Nature* **474**, 10–11; 2011), we coordinated the community of invasion biologists in a unique initiative to vote for a replacement.

We assessed more than 10,000 invasive species from the world's largest databases for their capacity to spread and for their potential ecological or economic impact. More than 650 experts from 63 countries then voted on the ten candidate species we shortlisted, and selected the giant salvinia (*Salvinia molesta*), an aquatic fern.

Native to Brazil, this fern has spread throughout the tropics and subtropics. It doubles in abundance within days, forming thick, floating mats that block light from expanses of water, reduce its oxygen content and degrade water quality. They also impede water-based transport, clog irrigation and power-generation systems, and harm local fisheries.

Now in the global spotlight, this new entrant to the IUCN list is set to increase public awareness of the harm caused by invasive species and to stimulate more discussion in science and policy circles.

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\*On behalf of 7 co-signatories. See [go.nature.com/wvjef2](http://go.nature.com/wvjef2) for full list.

## Avoid more organ transplant scandals

Our institution is launching an international transdisciplinary initiative to improve the lamentable state of solid-organ

transplantation in Germany and to help fulfil society's obligations towards millions of organ donors and recipients worldwide (see [go.nature.com/z5b7uo](http://go.nature.com/z5b7uo)).

The mortality rate following liver transplantation has risen alarmingly across the country over the past few years. The survival rate after one year is only 72% in Germany, which is 20% lower than in the United States and the United Kingdom, even though Germany has more transplant centres and fewer organ donors per capita (see [go.nature.com/pgmrpn](http://go.nature.com/pgmrpn); in German). Such scandals are leading to a steady decline in altruistic organ donations, with an 18% drop in the first quarter of this year compared with the same period in 2012.

The situation largely reflects the weak regulation of organ transplantation in Germany, especially by comparison with other countries such as the Netherlands and Denmark (C. Metz and N. Hoppe *Eur. J. Health Law* **20**, 113–116; 2013). Proposals to rectify this include setting up an independent institute of transplantation medicine that has regulative and standard-setting powers (see [go.nature.com/yzl4km](http://go.nature.com/yzl4km); in German).

A lack of good prognostic models compounds the likelihood of transplantation failure. Such models would allow clinical urgency to be weighed against transplantation outcome. We are therefore planning systematic multicentre trials to evaluate the prognostic value of liver-allocation scores.

Our initiative also aims to address the dearth of quality-management systems that are properly founded on comprehensive, evidence-based data and on precise methodology that considers patients' needs and expectations.

The early results are promising. We intend to publish regular updates to provide essential information to the transplantation community and

to ensure openness to the public.

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## Satellites: make data freely accessible

The cost of accessing satellite data is hampering the widespread application of satellite monitoring, a vital tool for controlling deforestation (Jim Lynch *et al. Nature* **496**, 293–294; 2013) and for biodiversity assessments. We urge government agencies that produce taxpayer-funded satellite images to make these available free of charge and in user-friendly formats.

Lynch and colleagues' call for daily satellite observations of forests worldwide would mean aggregating information from numerous satellites that are operated by many countries. Assembling the large data sets needed for global monitoring would be prohibitively expensive, however, because national governments do not have a free-access policy for their satellite images.

One solution would be to combine data from the US Landsat satellites with those from the European Space Agency's planned Sentinel-2 satellites, which could deliver optical imagery with global coverage every 3–5 days. The distribution of Landsat imagery has increased by two orders of magnitude since 2008, when the US Geological Survey made all the data free to access online. Data from NASA's MODIS and all of their Earth-observation imagery are also available for free, as are data from the China–Brazil Earth Resources Satellite programme.

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\*On behalf of 14 co-signatories. See [go.nature.com/pfv6an](http://go.nature.com/pfv6an) for full list.

## Satellites: ambition for forest initiative

We disagree strongly with the suggestion by Jim Lynch and colleagues that the outputs of the Global Observation of Forest and Land Cover Dynamics panel and the Global Forest Observations Initiative “lack ambition and an understanding of the potential of satellites” (*Nature* **496**, 293–294; 2013).

As participants in these programmes and in the United Nations Programme on Reducing Emissions from Deforestation and Forest Degradation (UN-REDD), we aim to show how remote sensing can help systematic global monitoring to make REDD+ a reality in the context of wider societal engagement. (REDD+ is a climate-mitigation initiative under the UN Framework Convention on Climate Change (UNFCCC).)

We also question the feasibility of Lynch and colleagues' call for rapid-response satellite monitoring of deforestation to be enshrined in international law under the UNFCCC, given national sovereignty concerns and the fact that we are not yet in a position to mitigate the problems of cloud cover. Although radar can penetrate cloud, the technology cannot yet capture changes in forest ecosystems in a systematic and repeatable way.

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### CONTRIBUTIONS

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**Supplementary information to:  
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Full list of co-signatories to a Correspondence published in *Nature* **498**, 37 (2013);  
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# Spatial distribution and range expansion of the Tawny Coster butterfly in South-East Asia and Australia

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# Spatial distribution and range expansion of the Tawny Coster butterfly, *Acraea terpsicore* (Linnaeus, 1758) (Lepidoptera: Nymphalidae), in South-East Asia and Australia

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**Abstract.** 1. Documenting the range size and range boundaries of species, and understanding the factors determining changes in these spatial components, is crucial given current rates of anthropogenic climate change and habitat loss. Here, we document the establishment of the acraeine butterfly, *Acraea terpsicore*, in South-East Asia (Indonesian islands south of Malay Peninsula, and Timor) and Australia for the first time. We estimate its rate of colonisation and potential for further range expansion in the Indo-Australian region according to bioclimatic niche models.

2. We modelled the potential distribution of the species in the Indo-Australian region under current climatic conditions and in 2050 following climate change. The bioclimatic niche models were based on five different modelling techniques, three global circulation models (GCMs) and two CO<sub>2</sub> emission scenarios (SRES), yielding 30 individual models that were combined in a consensus model.

3. *Acraea terpsicore* became established in Indo-China (Thailand) during the 1980s and since that time it has spread to other parts of South-East Asia. It was first recorded on the Australian mainland in the Northern Territory in April 2012 and within a few months of detection was found to occur at six locations, with an estimated extent of occurrence of 4000 km<sup>2</sup>. Thus, the range size of *A. terpsicore* has expanded by approximately 6000 km across the equator (c. 32 degrees latitude) in 28 years, with an average rate of colonisation (from Thailand to Australia) of 200 km year<sup>-1</sup> (range: 170–230 km year<sup>-1</sup>).

4. The bioclimatic niche models identified additional regions with favourable climatic conditions, and within Australia it is likely to occupy coastal and sub-coastal savannah woodlands of the entire monsoon tropics, indicating potential for further range expansion. Moreover, the species' potential range is likely to increase with climate change.

5. We hypothesise that habitat modification, particularly rapid deforestation of tropical forest in South-East during the past three decades, is a major factor accounting for the range expansion given the species' habitat preference for dis-

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turbed and open degraded areas. Climate change may be a contributing factor but is unlikely the sole determinant given the spatial area involved and rate of spread.

**Key words.** Bioclimatic niche modelling, biogeography, biological invasion, climate change, consensus model, invasive species.

## Introduction

Understanding the factors determining the spatial distribution of organisms, especially those influencing changes in their geographical range over time, is a fundamental element of ecology, biogeography and conservation biology. Quantifying the range size and range boundaries (in both latitude and altitude) of species, and assessing any shifts in these components, has perhaps never been more critical given contemporary rates of anthropogenic climate change and habitat loss, two factors that are rapidly modifying the spatial distribution of plants and animals world-wide (e.g. Parmesan *et al.*, 1999; Warren *et al.*, 2001; Hill *et al.*, 2002; Parmesan & Yohe, 2003; Thomas *et al.*, 2004, 2006; Brook *et al.*, 2008; Thomas, 2010; Gibson *et al.*, 2011; Bellard *et al.*, 2012).

Australia, in part because of its geographical isolation and relatively recent occupation by Europeans (since 1788), has in some ways served as a ‘laboratory’ to monitor changes in the spatial distribution of species, particularly the introduction and subsequent expansion of alien organisms. The continent has a long history of non-indigenous plants and animals entering the country (Groves & Burdon, 1986; Low, 2001), and these arrivals have either been intentional (e.g. introduction of African grasses for the pastoral industry; Cane Toad for the control cane beetles) or accidental (e.g. tramp ants, such as the Red Imported Fire Ant, *Solenopsis invicta* Buren, 1972). In other cases, species have arrived naturally via long-distance dispersal, perhaps one of the best known examples being the Monarch butterfly, *Danaus plexippus* (Linnaeus, 1758) (Clarke & Zalucki, 2004). A significant portion of these alien species have become invasive to the extent that they have developed weed or pest-like status and are now considered major threatening process to the survival of the continent’s unique biodiversity and integrity of ecosystem function (Low, 2001). Not surprisingly, extensive resources have been allocated and management strategies developed against biological invasions, from prevention through early detection and eradication to long-term containment and control (Simberloff *et al.*, 2013).

Among the insects, it is estimated that numerous alien species arrive on the Australian continent through various modes of importation, but few actually colonise (founder population persists temporarily) or become established (population persists permanently), and even fewer become invasive to the extent that they become economically important pests or have adverse ecological impacts (New, 1994, 2011). For the butterflies, there are few examples of non-indigenous species or subspecies entering the

Australian mainland (Table 1). At least seven butterfly taxa from the Oriental and/or Pacific regions appear to have reached the continent naturally as rare vagrants or possibly migrants via long-distance dispersal; these taxa are not known to breed on the Australian mainland, having been recorded from only one or a few specimens (Common & Waterhouse, 1972, 1981; Edwards, 1977; Braby, 2000; Lambkin, 2009; Braby *et al.*, 2010). At least two butterfly species – European Painted Lady, *Vanessa cardui* (Linnaeus, 1758) and Rice Swift, *Borbo cinnara* (Wallace, 1866) – have colonised the continent, but they do not appear to have become established (Angel, 1951; Common & Waterhouse, 1972, 1981; Braby, 2000; Meyer *et al.*, 2006). In contrast, the lycaenid *Strymon bazochii* (Godart, 1824) was intentionally introduced to Australia in 1914 as a potential biocontrol agent of *Lantana camara* L., but it failed to colonise and establish (Julien, 1987; Edwards, 1996; Day, 2012).

Prior to 2012, only two species of butterflies that entered Australia have become established. The Monarch, *Danaus plexippus*, occurs naturally in the New World and is not a native species in Australia; it became established in the early 1870s (following propagation of its main milkweed larval food plant, *Asclepias curassavica* L., along the eastern coast), and the most likely source of the founder population was from Vanuatu and/or New Caledonia from which it is hypothesised that large numbers of adults were transported across the Coral Sea by winds associated with a severe tropical storm depression (Clarke & Zalucki, 2004). It now occurs widely throughout much of the eastern, south-eastern and south-western regions of the continent. The Cabbage White, *Pieris rapae* (Linnaeus, 1758), was accidentally introduced from Europe (possibly via New Zealand) to Melbourne, Victoria, in the 1930s (Peters, 1970; Braby, 2000); today, it is well established throughout much of the temperate areas of the continent and is a major invasive pest of cruciferous crops and vegetable gardens.

The Tawny Coster, *Acraea terpsicore* (Linnaeus, 1758), is another non-native butterfly that has recently entered Australia (Sanderson *et al.*, 2012; Braby, 2013); however, unlike most of the examples noted above this species became established after colonisation. *A. terpsicore* is otherwise endemic to lowland areas of India and Sri Lanka (Doubleday & Westwood, 1846–1850; Bingham, 1905; Bell, 1910; Talbot, 1947; Wynter-Blyth, 1957) and until very recently was not known to occur south of the equator. In the past few decades, however, it has become widely established in the northern part of South-East Asia (Takanishi, 1988; Chou, 1994; Nishimura, 1994;

**Table 1.** Incursions of butterflies onto the Australian mainland and their mode of arrival and residential status.

Taxon	Natural geographical range	Mode of arrival	Status	Reference
<i>Borbo cinnara</i>	Asia, SE Asia, western Pacific islands	Not known	Colonised	Angel (1951), Braby (2000), Meyer <i>et al.</i> (2006)
<i>Belenois java peristhene</i>	Loyalty Island, New Caledonia, Norfolk Island	Natural dispersal	Vagrant	Common and Waterhouse (1972, 1981), Braby (2000)
<i>Appias albina infuscata</i>	Sumbawa (Indonesia)	Natural dispersal	Vagrant	Braby <i>et al.</i> (2010)
<i>Pieris rapae rapae</i>	Europe, North Africa, North Asia	Accidental introduction	Established (invasive)	Peters (1970)
<i>Danaus chrysippus cratippus</i>	Lesser Sunda Islands, Maluku	Natural dispersal	Vagrant	Common and Waterhouse (1981), Braby (2000), Lambkin (2009)
<i>Danaus plexippus</i>	North and Central America	Natural dispersal	Established (non-invasive)	Clarke and Zalucki (2004)
<i>Euploea climena macleari</i>	Indonesia, Christmas Island	Natural dispersal	Vagrant	Common and Waterhouse (1972, 1981), Braby (2000)
<i>Acraea terpsicore</i>	India, Sri Lanka	Natural dispersal	Established	This work
<i>Vanessa cardui</i>	Europe, North America, Africa, Asia	Natural dispersal	Colonised	Common and Waterhouse (1972, 1981), Braby (2000)
<i>Junonia erigone walkeri</i>	Indonesia, East Timor	Natural dispersal	Vagrant	Edwards (1977)
<i>Hypolimnas anomala albula</i>	Asia, SE Asia	Natural dispersal	Vagrant	Common and Waterhouse (1972, 1981), Common (1978), Braby (2000)
<i>Charaxes andrewsi</i>	Christmas Island	Natural dispersal	Vagrant	Common and Waterhouse (1972, 1981), Braby (2000)
<i>Strymon bazochii</i>	Central America	Intentional introduction	Failed to colonise/establish	Julien (1987), Edwards (1996), Day (2012)

Arshad *et al.*, 1996; West, 1996; Pierre & Bernaud, 1997; Huang, 2002; Tung, 2002). More recently, it has been reported from Indonesia (Matsumoto *et al.*, 2012), and in 2012 it was detected in Timor and Australia for the first time.

The major larval food plants of *A. terpsicore* are Passifloraceae (*Passiflora*, *Adenia*) (Bingham, 1905; Bell, 1910; Talbot, 1947; Wynter-Blyth, 1957; Pierre & Bernaud, 1997; Robinson *et al.*, 2001; Matsumoto *et al.*, 2012), Violaceae (*Hybanthus*, *Viola*) (Ramana *et al.*, 1997; Atluri *et al.*, 1999; Kaur *et al.*, 2009; Das *et al.*, 2010) and apparently Cucurbitaceae (Moore, 1880-1881; Marshall & De Niceville, 1882; Woodhouse, 1952; Wynter-Blyth, 1957; D'Abbrera, 1985, 1998; Robinson *et al.*, 2001; Wikramanayake & Wikramanayake, 2006). Robinson *et al.* (2001) also listed Bignoniaceae, Malvaceae, Moraceae and Verbenaceae, but the suitability (and reliability) of these records remains to be confirmed. In Australia, the larvae of *A. terpsicore* primarily exploit the native seasonal perennial herb *Hybanthus enneaspermus* (L.) F. Muell. (Violaceae), which they decimate, and very rarely the exotic vine *Passiflora foetida* L. (Passifloraceae) (Braby, Thistleton & Neal, unpubl. data). Both plants are widespread in the Oriental and Australian Regions. Despite its rapid rate of spread into geographical areas that were previously unoccupied, it is not certain if *A. terpsicore* qualifies as an 'invasive' species because its economic and biological diversity impacts have not been

assessed. Nevertheless, *A. terpsicore* is reputed by local market gardeners in Sri Lanka to be considered a pest of various gourds (Cucurbitaceae) (Woodhouse, 1952; D'Abbrera, 1985, 1998; Wikramanayake & Wikramanayake, 2006), and in northern Australia the Glasswing, *Acraea andromacha* (Fabricius, 1775), uses *H. enneaspermus* as a larval food plant (Braby, 2000, 2011) and thus potentially may be outcompeted by *A. terpsicore*. According to the glossary of the International Plant Protection Convention (ISPM 5, 2012), an alien invasive species is defined as 'an alien species that by its establishment or spread has become injurious to plants, or that by risk analysis is shown to be potentially injurious to plants'. Under these criteria, *A. terpsicore* would qualify as an invasive species (at least in Australia) because it has established, is spreading and the larvae injure (severely deplete) its host plant *H. enneaspermus*.

The purpose of this article is to review the incidence of *A. terpsicore* in South-East Asia (south of the Malay Peninsula), with the aim of circumscribing its current spatial distribution (range size). We then document its occurrence within the Northern Territory of northern Australia, and predict what its potential range in South-East Asia and Australia might be under current climatic conditions and following climate change (2050) using bioclimatic niche models. We also estimate its rate of colonisation, and briefly discuss factors that may have contributed to its expansion over the past three decades.

## Materials and methods

### Sources of distribution data

Sources of distributional data for South-East Asia and Australia were obtained from the scientific literature, museum specimen records and the internet. Records for India, Sri Lanka, Thailand and Vietnam were obtained primarily from Pierre and Bernaud (1997), who published a detailed map of *A. terpsicore* for the region. Additional literature records since that publication include those by Atluri *et al.* (1999), Das *et al.* (2010) and Kaur *et al.* (2009) for India, and Arshad *et al.* (1996), Tung (2002), Aoyama and Kaito (2009) and Bernard (2010) for the Malay Peninsula. With the exception of the recent paper by Matsumoto *et al.* (2012), records for South-East Asia (south of the Malay Peninsula) were largely obtained from internet sites that refer to photographic records or provide evidence of the species in the Greater and Lesser Sunda Islands (see Appendix S1). Records for Timor and Australia were based on material registered in the following repositories:

- 1 ANIC: Australian National Insect Collection, Canberra, Australia
- 2 DAFF: Biosecurity, NAQS Invertebrate Collection, Darwin, Australia
- 3 NTM: Museum and Art Gallery of the Northern Territory, Darwin, Australia
- 4 NTEIC: Northern Territory Economic Insect Collection, Berrimah, Australia

These records provided a total of 89 occurrence points, which were used in the spatial analysis. The spatial precision for these data points varied from 10 m to more than 1 km. Because we were interested in only broad patterns of potential range, fine-scale data were not critical in the analysis. The spatial distribution and extent of occurrence (EOO) in Australia were estimated by calculating the minimum convex polygon based on Geographic Information System analysis using ArcGIS 10, ArcMap Version 10.0 software.

Two model outputs for the Indo-Australian region were generated: (i) under current climatic conditions, and (ii) in 2050. The second model was generated to determine the species' potential geographical range to expand even further under future climatic conditions. The spatial distribution of the butterfly in Australia was then compared with that of its larval food plant, *H. enneaspermus*, based on data (788 occurrence points) in CHAH (2009).

### Ecological niche modelling

The bioclimatic niche models were based on the 89 occurrence points (presence-only data) of *A. terpsicore*, both from invaded and native habitats (see Broennimann *et al.*, 2007; Beaumont *et al.*, 2009). For models requiring absence data, 10 000 pseudo-absence points were

generated randomly from around the world to provide background data.

Five machine learning modelling techniques were used to generate the consensual forecasts (see Bertelsmeier *et al.*, 2013): one-class Support Vector Machines (SVM) (Cristianini & Schölkopf, 2002) two-class SVM (Franklin, 2009), Artificial Neural Networks (ANN) (Maravelias *et al.*, 2003; Franklin, 2009), classification trees (CT) averaged over 10 iterations of the model algorithm (De'ath & Fabricius, 2000) and MaxEnt, (Phillips *et al.*, 2006). All models were run using the ModEco Platform with default parameters (Guo & Liu, 2010).

A limitation of modelling is that outputs are dependent on the specifically chosen input data (Buisson *et al.*, 2010); in this case, the algorithms, global climate models and scenarios of human development. To minimise potential resultant variation, we conducted consensual forecasts (Araújo & New, 2007) by combining 30 individual model forecasts, based on the five different modelling techniques described above and three Global circulation (climate) models (GCMs), each with two Special Report on CO<sub>2</sub> Emission Scenarios (SRES). The goal of consensual forecasts is to separate the signal from the 'noise' associated with errors and uncertainties of individual maps based on individual model outputs (Araújo & New, 2007). The individual model outputs (i.e. probability of presence in each pixel) were weighted according to their AUC score (see below). We obtained a continuous projection of the consensus model with a probability of the species being present assigned to each pixel.

### Climatic predictors

We modelled the species niche based on the 19 bioclimatic variables provided by the WorldClim database (Hijmans *et al.*, 2005). The full set of bioclimatic variables were used as model input because the machine learning methods used for niche modelling implicitly deal with variable selection (Guyon & Elisseeff, 2003; Elith *et al.*, 2011). Machine learning methods learn the mapping function or classification rule inductively from the input data (Elith *et al.*, 2006). The bioclimatic variables are derived from monthly temperature and rainfall values from 1960 to 1990, and represent annual trends, seasonality and extreme or limiting environmental factors (Hijmans *et al.*, 2005). We used a spatial resolution of 10 arcmin (approximately 18.5 km × 18.5 km pixel).

Future climatic data for 2050 were sourced from the 4th IPCC assessment report (IPCC, 2007). The projections were calibrated and statistically downscaled using the WorldClim data for current conditions so that the projections can be compared. We used downscaled climate data from three GCMs: the CCCMA-GCM2, CSIRO-MK2 and HCCPR-HADCM3 (IPCC, 2007). Similarly, we used the two extreme SRES: the optimistic B2a scenario (CO<sub>2</sub> concentration 800 ppm, 1.4–3.8 °C temperature increase) and the pessimistic A2a scenario (CO<sub>2</sub>

concentration 1250 ppm, 2–5.4 °C temperature increase) (IPCC, 2007).

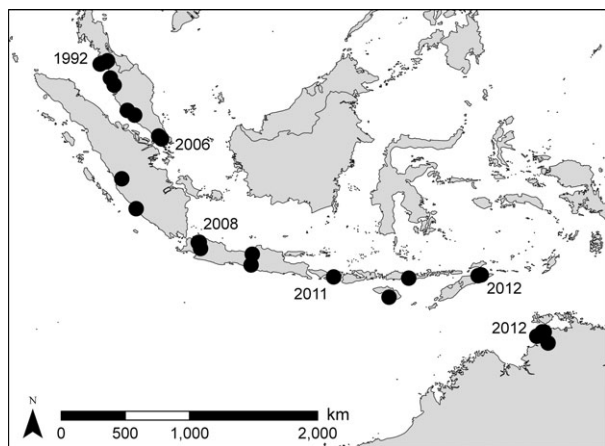
#### Model validation

Model robustness was evaluated using the AUC, which is a non-parametric threshold-independent measure of accuracy commonly used to evaluate species distribution models (e.g. Pearce & Ferrier, 2000; Roura-Pascual *et al.*, 2009). AUC values range from 0 to 1: scores between 0.5 and 0.7 are considered low, 0.7–0.9 moderate and >0.9 high (Franklin, 2009). Accuracy assessment was carried out with 10 fold cross-validation.

## Results

#### Distribution records in South-East Asia (south of Malay Peninsula)

The only published record of *A. terpsicore* from Indonesia and adjacent areas we are aware of is the recent paper by Matsumoto *et al.* (2012) who documented its presence on Lombok; however, there are numerous unpublished ‘citizen science’ records on the internet (e.g. Khew, 2008; Haliaster Nature Club, 2012) that refer to photographic records or provide evidence of the species in Singapore, Sumatra, Java, Flores and Sumba, all of which indicate its presence in the Greater and Lesser Sunda Islands of South-East Asia south of the Malay Peninsula (Fig. 1; see also Appendix S1 for more detailed compilation). There is also a specimen in the Museum Zoologicum Bogoriense, Jalan Raya Jakarta-Bogor, collected



**Fig 1.** Distribution of *Acraea terpsicore* in South-East Asia (south of Thailand) and north-western Australia, showing known locations (black circles) (see Appendix S1 for locality records and associated data). Years of detection (first recordings) are indicated for each country (i.e. Malaysia, Singapore, Indonesia (Greater Sunda, Lesser Sunda), East Timor, Australia).

from near Padang, Sumatra labelled ‘Mt. Kerinci, 21 March 2009, Pak Dahelmi’ (Djunijanti Peggie, pers. comm.). In East Timor, V. Kessner (pers. comm.) recorded *A. terpsicore* in May 2012 and he found the species to be abundant and widespread on the island (voucher material in NTM from 2 km E Vemassee, Baucau District and Watabo Beach approximately 4 km N Baucau, Baucau District). Subsequently, R. Willan and N. Wright (pers. comm.) recorded the species at Dili in October 2012 (Appendix S1).

#### Distribution records in Australia

In Australia, *A. terpsicore* was first recorded in the Northern Territory on the Cox Peninsula at three sites at Wagait Beach on 9 April 2012 (Table 2). Subsequently, the species was recorded at Dundee Beach, Belyuen Community approximately 13 km SSW of Wagait Beach, near Adelaide River, Charles Darwin National Park near the city of Darwin, Holmes Jungle Nature Park in the outer north-eastern suburbs of Darwin, and in the suburb of Herbert in the Darwin Rural Area. Thus, during the year 2012, *A. terpsicore* was recorded from six discrete locations in northern Australia (Table 2), with evidence of breeding at three of these locations (Wagait Beach, Adelaide River, Darwin). The six locations indicate an EOO of approximately 4000 km<sup>2</sup> (Fig. 2).

Wagait Beach was visited on 26 January 2011, but the butterfly was not recorded at that time, suggesting that the arrival to Australia was recent and probably occurred during the 2011–2012 wet season (i.e. a few months before its detection in April 2012).

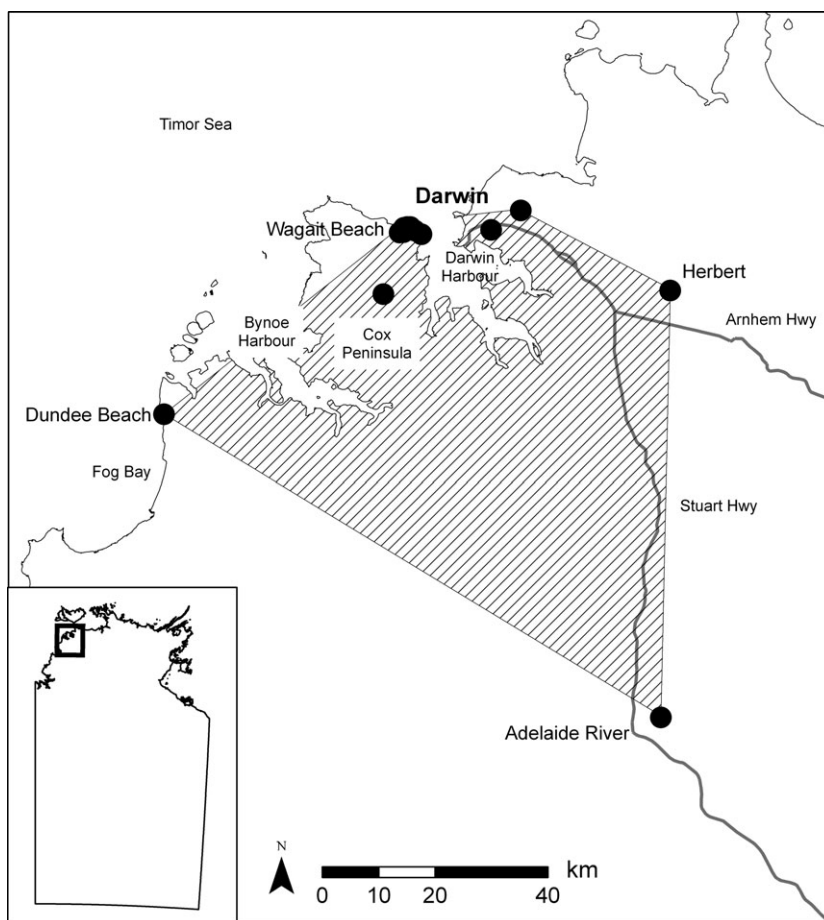
#### Rate of colonisation

Takanishi (1988) first recorded *A. terpsicore* from Thailand based on five specimens collected from near Chonburi in March 1988; however, a report by West (1996), who recorded the species at Chiang Mai in April 1984, appears to be the earliest record for that country. From northern Thailand, it was subsequently recorded farther south in central Thailand (at Chonburi in March 1988) (Takanishi, 1988; Nishimura, 1994) and the Malay Peninsula, where it was first detected at Perlis in December 1992 (Arshad *et al.*, 1996), and then farther east in Laos (Nakamura & Wakahara, 2012), Vietnam (at Qui Nhon and Dinh Quan in May 1992) (Nishimura, 1994; Pierre & Bernaud, 1997) and Hainan of southern China (Chou, 1994; Huang, 2002). As noted above, it was first recorded in Australia near Darwin in April 2012 (Sanderson *et al.*, 2012).

Given these dates of first detection, it is instructive to estimate the speed at which the butterfly is spreading, although we acknowledge that the species may have reached a given location for some months (or even years) before it was detected. Hence, calculations of rates of

**Table 2.** Locations and sites at which adults of *Acraea terpsicore* were recorded in the Northern Territory, Australia, during 2012. Dates represent time of first detection. Coordinates are in decimal degrees and datum WGS84.

Location	Site	Latitude (°S)	Longitude (°E)	Date	Observer
Wagait Beach	Wagait Tower Rd	-12.42915	130.74791	9 April 2012	C. Sanderson
Wagait Beach	Erickson Cres	-12.43757	130.73690	9 April 2012	C. Sanderson
Wagait Beach	approximately 2 km W of shop	-12.43799	130.73100	9 April 2012	C. Sanderson
Wagait Beach	Baluria Rd	-12.42929	130.74271	23 May 2012	M.F. Braby & B. Thistleton
Wagait Beach	Cox Dve	-12.43029	130.73788	23 May 2012	M.F. Braby & B. Thistleton
Wagait Beach	De Lissa Dve	-12.43491	130.75522	23 May 2012	M.F. Braby & B. Thistleton
Wagait Beach	Mandorah, near Charles Point Rd	-12.44074	130.76558	23 May 2012	M.F. Braby & B. Thistleton
Dundee Beach	Marege Dve	-12.72850	130.35521	19 April 2012	M.F. Braby & K. Brennan
Adelaide River	Haynes Rd	-13.21222	131.14750	22 April 2012	M.F. Braby
Belyuen Community		-12.53642	130.70508	19 July 2012	G. Bellis & S. Anderson
Darwin	Charles Darwin NP (near park entrance)	-12.43393	130.87682	28 May 2012	M. Neal
Darwin	Holmes Jungle NP (Vanderlin Dve)	-12.40277	130.92386	22 December 2012	M.F. Braby
Herbert	Daniel Cct	-12.53055	131.16222	24 December 2012	D. Bisa

**Fig 2.** Distribution of *Acraea terpsicore* in the Northern Territory, Australia, showing known locations (black circles) and extent of occurrence (cross-hatched area) based on records for 2012 (see Table 2). Inset map shows the Northern Territory.

colonisation are minimum estimates, although it should be pointed out that expansions are typically characterised by an invasion front of increased abundance, which is relatively easy to detect. The distance from Thailand (Chiang Mai) to Malaysia (Perlis) over land is approximately 1500 km; given that it took about 8.7 years for the butterfly to reach the Malay Peninsula from northern Thailand, this translates to a minimum dispersal rate of approximately  $170 \text{ km year}^{-1}$ . The distance from Malaysia (Perlis) to north-western Australia (Darwin) via the Greater and Lesser Sunda Islands is approximately 4500 km; given that it has taken about 19.3 years for the butterfly to reach the Australian mainland from the Malay Peninsula, this translates to a minimum dispersal rate of approximately  $230 \text{ km year}^{-1}$ . These two estimates yield an average rate of colonisation of  $200 \text{ km year}^{-1}$ , although its rate may have accelerated during the past decade once it colonised islands south of the Malay Peninsula (Fig. 1). The two estimated minimum dispersal rates in South-East Asia ( $170$  and  $230 \text{ km year}^{-1}$ ) are not only of similar order of magnitude but also remarkably close to one another.

#### Spatial modelling in South-East Asia and Australia

Outputs from the bioclimatic models are shown in Fig. 3. Model accuracy for all five ecological niche models varied from very good to excellent according to AUC. AUC varied from 0.851 (SVM1) to 0.966 (ANN).

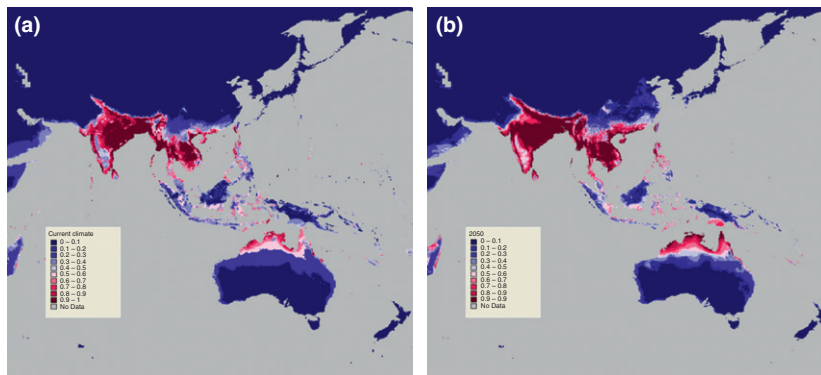
Our simulations under current climatic conditions (Fig. 3a) predicted a much wider potential range than the species' current geographical range. The bioclimatic models indicate that in addition to the known range in India, Sri Lanka and Indo-China, favourable areas occur in the intervening areas of Burma and Cambodia, as well as in South-East China and Taiwan, through the Philippines,

Sulawesi and Maluku to northern Australia. We also identified climatically favourable areas in Central and South America, Africa and Madagascar (data not shown). The projected distribution under global warming models (predicted for 2050) showed that the potential range was likely to increase, with likely occupancy in the lowland areas of southern New Guinea and islands of the South-West Pacific, such as New Caledonia (Fig. 3b).

Within Australia, *A. terpsicore* is likely to occupy the whole of the monsoon tropics, including the Kimberley, WA, northern areas of the 'Top End' of the Northern Territory (i.e. the northern portion above approximately  $16^{\circ}\text{S}$  latitude), coastal areas of the Gulf Country and parts of Cape York Peninsula, Queensland (Fig. 4). It is also likely to occur sporadically along the coastal areas of north-eastern Queensland, including the Wet Tropics and as far south as the Tropic of Capricorn in the Yeppoon-Byfield area near Rockhampton. Comparison of this projected range of the butterfly with the known spatial distribution of the primary larval food plant *H. enneaspermus* suggests a much narrower range than its host (Fig. 4). There was considerable congruence in northern Australia, but the food plant extends farther south-east, reaching the coastal areas of north-eastern New South Wales, as well as into semi-arid areas of the Northern Territory and Queensland. Therefore, the species' distribution is unlikely to be limited by the distribution of the larval food plant.

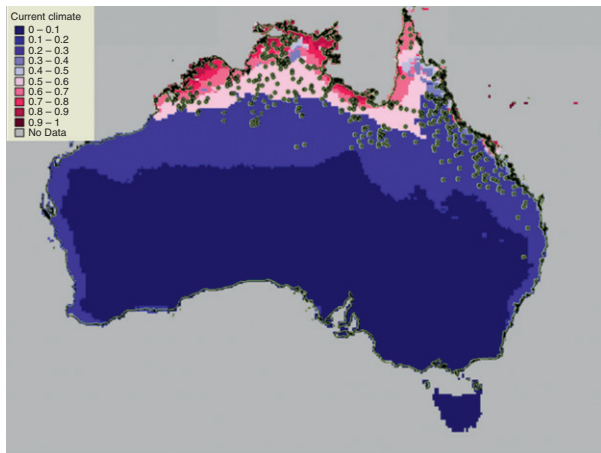
#### Discussion

The natural distribution of *A. terpsicore* is India and Sri Lanka; however, in recent decades, the species has been reported from South-East Asia, including Thailand (Takanishi, 1988; Nishimura, 1994; West, 1996; Pierre & Bernaud, 1997), Laos (Nakamura & Wakahara, 2012), Vietnam (Nishimura, 1994; Pierre & Bernaud, 1997),



**Fig 3.** Spatial model of *Acraea terpsicore* in the Indo-Australian region showing predicted geographical distribution (red shading) according to the following: (a) current climatic conditions, and (b) projected climatic conditions under global warming in 2050. Probability of occurrence for a given pixel (from 0 = very unlikely to 1 = very likely) is indicated in the legend. Areas where the probability of occurrence per pixel exceeds 0.5 are deemed potentially 'favourable', and these are shown in different shades of red. The maps show the consensual prediction based on the combination of six future climatic scenarios (3 GCMs, each with 2 SRES).





**Fig 4.** Spatial model of *Acraea terpsicore* in Australia showing predicted geographical distribution (red shading) according to current climatic conditions. Symbols (green circles) indicate spatial distribution of the larval food plant *Hybanthus enneaspermus* (data from CHAH, 2009). Probability of occurrence is indicated in the legend. The map shows the consensual prediction based on the combination of six future climatic scenarios (3 GCMs, each with 2 SRES).

Hainan (Chou, 1994; Huang, 2002) and the Malay Peninsula (Arshad *et al.*, 1996; Tung, 2002; Aoyama & Kaito, 2009; Bernard, 2010). Our investigations indicate that the species now occurs widely in areas south of Malaysia through Indonesia to East Timor and northern Australia. Pierre and Bernaud (1997) published a detailed map of *A. terpsicore* showing the known distribution of the species in India, Sri Lanka, Thailand and Vietnam based on available locality data at that time. Additional records since that publication for South-East Asia (south of Thailand) and northern Australia are shown in Fig. 1.

Ten years ago Tung (2002) warned that *A. terpsicore* was likely to disperse farther southwards from Malaysia, but noted that its rate of colonisation could not be accurately determined due to the lack of detailed recordings. Matsumoto *et al.* (2012) suggested that the species was expanding its range in Indonesia, noting that on Lombok the butterfly was absent during extensive surveys conducted in 2003–2006 but was abundant in 2011, with 64 specimens collected in grassland habitat during the months of January and October of that year. Chronological analysis of the limited spatial and temporal data suggests that species has indeed been dispersing south and east through South-East Asia (Fig. 1).

It is not clear how *A. terpsicore* became established in South-East Asia. Perusal of the scientific literature indicate that there are at least three hypotheses: (i) the species was accidentally and recently introduced to Indo-China from India/Sri Lanka (Nishimura, 1994), (ii) the species naturally expanded its range out of India and colonised Thailand via Myanmar (Burma) (West, 1996) and (iii) the species always existed in the region (e.g. Thailand and

Vietnam), but has since become more abundant and widespread as a result of modification in the environment through agriculture, the butterfly favouring cultivated regions and degraded forests where the larval food plants grow (Pierre & Bernaud, 1997; Tung, 2002). Available data appear to support either of the first two hypotheses. Support for the third hypothesis was based on an early record by Dubois and Vitalis de Salvaza (1919 p. 234) who listed “*Telchinia violae*” under the subfamily Acraeinae from Cochinchina (i.e. southern third of Vietnam when it was a French colony) in their checklist of Lepidoptera of Indo-China. No other evidence was provided to substantiate this record; however, since the authors also listed *Acraea vesta* Fabricius, 1787 (= *A. issoria* Hübner, 1816) (given as *Pereba vesta*), the only other species of acraeine to occur in South-East Asia, it is possible that the record is reliable. Another possibility (fourth hypothesis) is that *A. terpsicore* was intentionally introduced into Thailand in a similar way that the heliconiine *Dryas iulia* (Fabricius, 1775) became established in Thailand (Ek-Amnuay, 2012). During the late 1990s, live adults of this Neotropical butterfly were maintained in a commercial butterfly house in Phuket, from which it is believed that it escaped. The larvae of *D. iulia* feed on Passifloraceae and the butterfly has now invaded the Malaysian island of Langkawi (Aoyama & Kaito, 2009; Ek-Amnuay, 2012).

The factors contributing to the range expansion and rapid spread of *A. terpsicore* in South-East Asia and northern Australia are not entirely clear. Is it responding to climate change to stay in equilibrium with its shifting climatic envelope, or is it responding to some other environmental change such as habitat loss, or is it an invasive species that has not reached its full potential range? Analysis of long-term data sets of temperate butterflies in the northern hemisphere have revealed for many species shifts in range size and/or range boundaries towards higher latitudes or altitudes consistent with predictions of global warming (Hill *et al.*, 1999, 2002; Parmesan *et al.*, 1999; Warren *et al.*, 2001; Thomas, 2010). For others, range sizes have contracted because of local extinctions and lack of suitable habitat in which to colonise (Warren *et al.*, 2001; Hill *et al.*, 2002; Thomas *et al.*, 2006). There have been no comparable studies in Australia, but modelling of the spatial distributions of butterflies suggests the range size of narrow-range endemics is likely to retract in response to climate change (Beaumont & Hughes, 2002). Predictions for lowland tropical species, however, are far less certain because of the complicating factor of water availability in determining spatial distributions, and the few empirical studies examining shifts in range sizes and boundaries at low latitudes have focused on taxa restricted to montane areas (see Thomas, 2010 for review). While past climate change may well be a contributing factor, this is unlikely to be the sole determinant given the spatial area involved – the range size of *A. terpsicore* has expanded over a distance of approximately 6000 km (c. 32 degrees latitude) across the equator, from Chiang

Mai (18°47'N) in the northern hemisphere to Adelaide River (13°14'S) in the southern hemisphere, in 28 years, with an average rate of colonisation of 200 km year<sup>-1</sup>.

A more likely explanation is habitat modification. The species' preferred habitat in both South-East Asia and northern Australia comprises highly modified open areas, such as cultivated regions, suburban roadsides, disturbed grassland (i.e. cleared woodland/forest that is regularly slashed or graded) and degraded savannah woodland. In these habitats, the larval food plants – *Passiflora foetida* in Vietnam and Lombok (Pierre & Bernaud, 1997; Matsumoto *et al.*, 2012) and *H. enneaspermus* in Australia (Braby, Thistleton & Neal, unpublished data) – grow in proliferation and are readily exploited by the butterfly. Following colonisation in Australia, the population in the Darwin region spread rapidly throughout the urban and outer Rural Areas during the 2012–2013 wet season to the extent that it was one of the most abundant and widespread butterflies in the modified suburban landscape (Braby, Thistleton & Neal, unpubl. data). These observations suggest that *A. terpsicore* is a pioneer species favouring early succession habitats. South-East Asia has the highest deforestation rate of tropical forest in the world, largely due to conversion of natural habitat for agriculture and timber production (logging) and degradation by catastrophic forest fires, and the rate of loss has accelerated during the past two decades (Sodhi *et al.*, 2004, 2010; Sodhi & Brook, 2006; Gibson *et al.*, 2011). In the Sundaland biodiversity hotspot (which includes the Malay Peninsula, Sumatra and Java, as well as Borneo), for example, more than 92% of the original extent of primary vegetation has been lost (Myers *et al.*, 2000). These land-use changes have led to profound losses of, and threats to, South-East Asia's unique tropical biodiversity. Conversely, for ecologically generalist or pioneer species, extensive deforestation, agricultural expansion and increased urbanisation during the past few decades may well have provided conditions favourable for colonisation.

Range expansions of butterflies in Australia have been well documented, particularly among a set of five species of HesperIIDae (*Hasora khoda haslia* Swinhoe, 1899, *Tagiades japetus janetta* Butler, 1870, *Ocybadistes walkeri sothis* Waterhouse, 1933, *Cephrenes augiades sperthias* (C. Felder, 1862), *C. trichopepla* (Lower, 1908)) (Hutchinson, 1988; Crosby & Dunn, 1989; Crosby, 1990, 1994; Dunn & Eastwood, 1991; Eichler, 1999; Braby, 2000; Peters *et al.*, 2010). Changes in the geographic range for these five species have been facilitated by ability of the larval stage to exploit non-natural larval food plants that have been established/propagated outside the natural range of the butterfly, and sometimes have been aided by human-assisted transportation. Nevertheless, incursions of butterfly species into Australia, either by introduction (accidental or intentional) or through natural long-distance dispersal, appear to be rare (Clarke & Zalucki, 2004). We estimate that at least 13 taxa (including 1 intentional introduction) have arrived on the mainland during the past 140 years, but only two of these (*Pieris rapae*, *Danaus plexippus*) have become

established, with *A. terpsicore* representing a third case (Table 1). Apart from the invasive *P. rapae*, the larvae of which feed on vegetable crops as well as cruciferous weeds, there are no known impacts of *D. plexippus* and *A. terpsicore* on biosecurity or biodiversity. Nevertheless, there is a possibility that *A. terpsicore* may prove to be an invasive species in Australia because of its apparent association with cucurbits (and hence potential threats to the horticultural industry) and its exploitation of *Hybanthus* (and hence potential impact on the native *A. andromacha*).

Bioclimatic models allow an assessment of future spread by identifying potentially suitable areas. Our spatial bioclimatic models, for both current climatic conditions and in 2050, predict that the geographical range of *A. terpsicore* is likely to expand and occupy much of northern Australia, as well as some coastal areas in north-eastern Queensland. These predicted areas are characterised by low topography and a seasonal climate of high moisture and high temperature relative to the rest of the continent. Moreover, the vegetation of Australian monsoon tropical biome is dominated by tropical savannah woodland (including open degraded areas) that supports an abundance of the larval food plant *H. enneaspermus*. A characteristic geographical pattern of this biome is that many plants and animals occur widely across northern Australia (Bowman *et al.*, 2010). Hence, it is very likely that the potential areas estimated for *A. terpsicore* will be realised because it matches the general distribution pattern for a suite of other species restricted to the region. Furthermore, the species' potential range is likely to increase with climate change, both in Australia and South-East Asia. Although *A. terpsicore* is currently already expanding its range, this might be further exacerbated by climate change because of the increase in extent of favourable areas. There are relatively few studies demonstrating an increase in geographical extent following climate change, but our result is consistent with the general view that climate change and biological invasions will act synergistically (Dukes & Mooney, 1999; Brook *et al.*, 2008; Hellmann *et al.*, 2008; Walther *et al.*, 2009).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12038:

**Appendix S1.** Records of *Acraea terpsicore* in South-East Asia (south of Thailand).

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# What is your favourite coke? An experiment with two invasive ant species

Cleo Bertelsmeier



## A3. Taste preferences in invasive ants

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### 1. INTRODUCTION

Invasive ants are among the world's worst invasive species (IUCN SSC Invasive Species Specialist Group, 2012; Lowe et al., 2000). They are known for their enormous impacts on biodiversity and ecosystem functioning (Holway et al., 2002; Lach and Hooper-Bui, 2010; Rabitsch, 2011). In addition, they are a nuisance to humans because they invade houses, destroy electrical equipment, can cause painful stings (IUCN SSC Invasive Species Specialist Group, 2012) and sometimes transmit diseases (Moreira et al., 2005). Further, they are agronomic pests and can reduce yields. This has led to enormous economic costs at a global scale (Pimentel et al., 2005). Invasive ants are notoriously difficult but several treatment options are currently being developed (Hoffmann et al., 2010). Any potential food source has to be attractive to the target ants. However, little is known about the food preferences of invasive ants. Generally, they are omnivorous (Holway et al., 2002), but their diet has a high percentage of sweet liquids (honeydew, extra-floral nectar) (Wilder et al., 2011). However, it remains to be elucidated if different invasive ants have preferences for different sugary resources. Moreover, ant invasions mostly occur in highly disturbed environments and are often associated with infrastructures (King and Tschinkel, 2008). Many invasive ants have established in cities where they are likely to share human food resources (at picnics etc). However, nothing is known so far about the relative attractiveness of different industrial sugary liquids to invasive ants, although they are likely to come in contact with this type of food resource very frequently. Here, I test the diet preferences of two invasive ants, the Argentine ant, *Linepithma humile*, also known as the 'sugar ant' (Holway et al., 2002), and the invasive garden ant, *Lasius neglectus* (Cremer et al., 2008). Our aim is to test the preferences of these ant species for different types of coca cola, which is one of the most popular human soft drinks. Coca-cola is the world's largest beverage company, with 1.7 billion servings consumed each day (Kent et al., 2011). In addition, coca cola is sold in every country on Earth, except Cuba and North Korea, which makes it very likely that both ant species can come in contact with this soft drink throughout their invasive range. I set up a lab experiment with 6 different types of coca cola 1) classic coke, 2) caffeine-free coke, 3) cherry coke, 4) vanilla coke, 5) coca light, 6) coca zero and also sugarwater and normal water. I recorded the total number of workers that visited each of the baits, the maximum number of workers present simultaneously at each of the baits and the time it took a colony to recruit to each of the baits.

### 2. MATERIAL AND METHODS

#### *Colony collection and maintenance of laboratory colonies*

The ants were collected in April 2012 in Southern France. Colony fragments were maintained in plastic nest containers (55x 35x 25 cm) filled with substrate from the original nesting site (soil, wood, leaves) and contained several tubes of water. The boxes were kept at  $24 \pm 2^\circ\text{C}$  with the appropriate soil moisture. The ants were fed daily with a variant of the Bhatkar diet (Dussutour and Simpson, 2008).

#### *Baiting experiment*



Prior to the experiment, the ants were starved for one week. Subsequently, a colony of 150 workers and one queen was aspirated and placed into a small plastic nest (6 x 7 x 4 cm), filled with plaster at an appropriate humidity (Fig 1). The entrance of the nest was blocked and the ants were allowed to acclimatize for 24h, before the piece of rubber was removed and the ants were allowed access to the foraging arena. Eight baits (coca cola, cherry coke, vanilla coke, caffeine-free coke, coca light, coca zero, sugarwater and water) of 1ml each, were placed in a random order on aluminium foil at a distance of approximately 6 cm from the nest entrance. We recorded foraging behaviour every three minutes for one hour. I recorded the maximum number of workers observed simultaneously at a bait, the total number of workers observed at a bait, and a recruitment score (total time of the experiment – time at which at least five workers are present simultaneously at the bait). After each experiment, the foraging arena was cleaned and pheromone traces were eliminated with alcohol. Each colony was only used in one single trial. I carried out eight replicates per species.

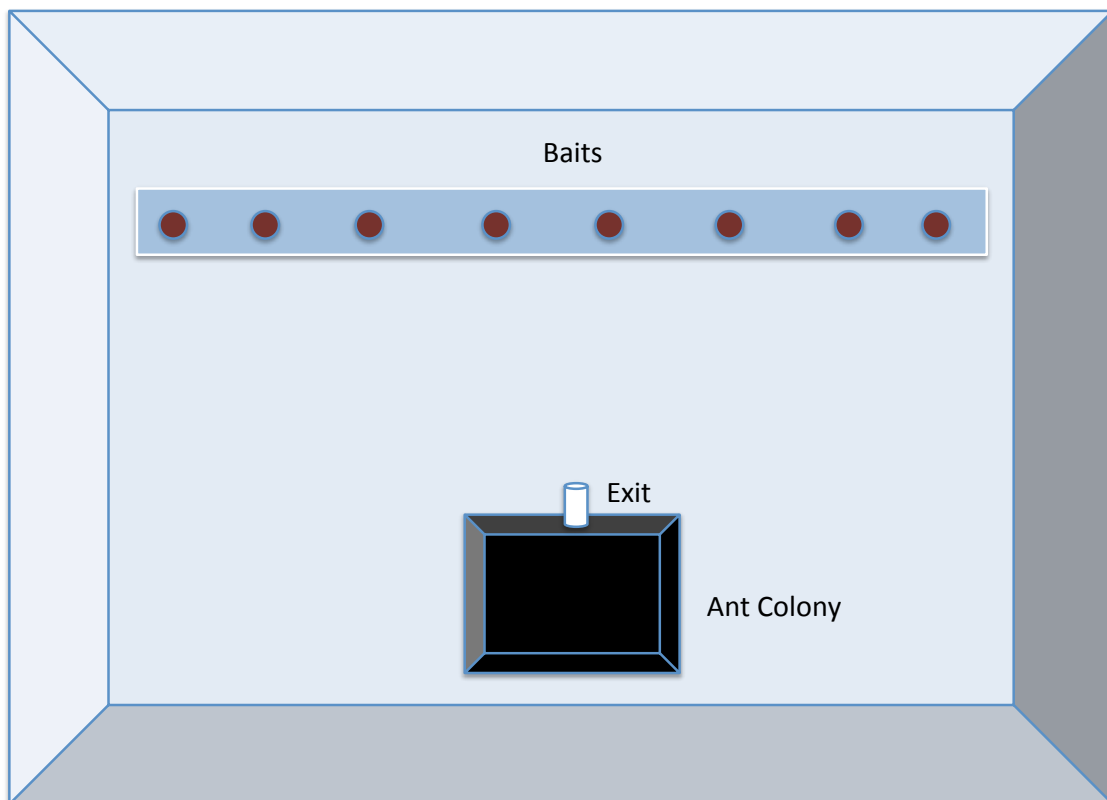


Fig. 1 Experimental set-up

### Analyses

Prior to statistical analysis of the differences in SI, KI and DI among species, I examined all data distributions using the Shapiro Wilk W test for normality. Data for the recruitment score did not follow a normal distribution. Therefore I used the nonparametric Kruskal-Wallis rank sum test, adjusting for multiple comparisons with a Kruskal multiple comparison test of the `kruskalmc()` function included in the `pgirmess` package in R. The other variables (maximum

and total number of workers) followed a normal distribution. I analysed differences among drinks with an ANOVA, adjusting for multiple comparisons using the Tukeys honest significance test (HSD). I conducted a two-way ANOVA to test whether the difference in total number of workers recorded at different drinks depended on the species. All analyses were carried out using R v.2.15.2

### 3. RESULTS

Drinks differed greatly in their attractiveness to the invasive ant species. Both species, *L. humile* and *L. neglectus*, never visited the following drinks: water, coca zero, coca light and sugarwater. Both species visited only classic coke, cherry coke, vanilla coke and caffeine-free coke. All subsequent analyses comparing preferences of different drinks are therefore based on a comparison among these four drinks.

#### *L. neglectus*

The invasive garden ant did not show a significant preference for any of the four types of sugary coca cola (Fig 2). There were no significant differences in the total number of workers that visited different drinks ( $F_{(3,28)}=0.1373$ ,  $p=0.9369$ ), nor in the maximum number of workers on different drinks ( $F_{(3,28)}=0.37$ ,  $p=0.7752$ ), nor among recruitment speeds ( $F_{(3,28)}=0.5897$ ,  $p=0.8988$ ).

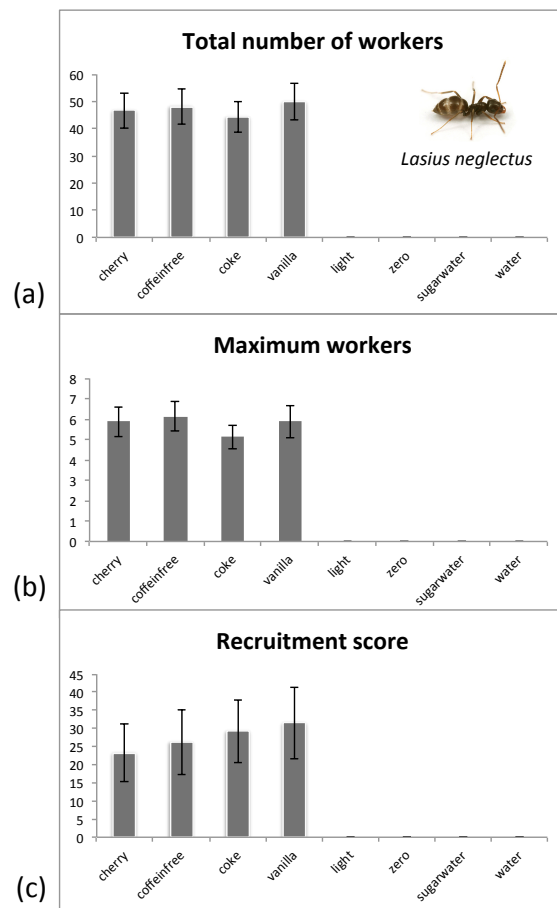


Fig. 2 *Lasius neglectus*

#### *L. humile*

The total number of Argentine ant workers found at the baits differed significantly among drinks ( $F_{(3,28)}=104.6$ ,  $p<0.0001$ ). The highest number of workers visited cherry coke, followed by caffeine-free coke and vanilla coke, and finally classic coke (Fig 3a). Further, the maximum number of workers present simultaneously on one drink differed significantly among drinks ( $F_{(3,28)}=5.668$ ,  $p=0.0037$ ). The highest maximum number of workers was found on cherry coke, followed again by caffeine-free coke and vanilla coke, and finally classic coke (Fig. 3b). In addition, the recruitment speed differed among drinks ( $\chi^2_{(3)} = 13.3002$ ,  $p=0.004$ ). The recruitment to cherry coke was fastest, followed by caffeine-free coke and vanilla coke and slowest to classic coke (Fig. 3c).



Fig. 3 *Linepithema humile*

A two-way Anova revealed a significant interaction of species and drink ( $F_{(10, 7/ 56)}$ ,  $p<0.0001$ ) (Fig. 4). *L. humile* was significantly more attracted to cherry coke than *L. neglectus*. On the other hand *L. neglectus* was significantly more attracted to classic coke (Fig. 4)

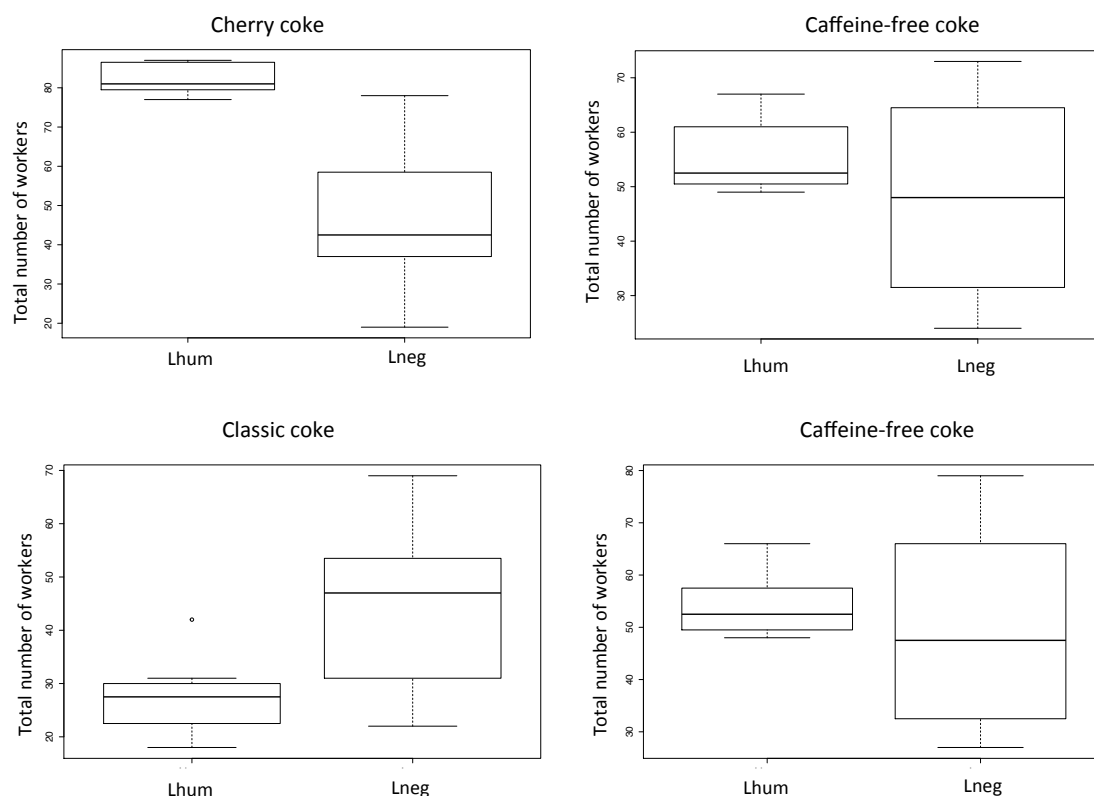


Fig. 4 Species comparison between *L. humile* (Lhum) and *L. neglectus* (Lneg) in the number of workers attracted to different drinks.

#### 4. DISCUSSION

The Argentine ant and the invasive garden ant showed diet preferences. None of the species visited water or drinks with artificial sweeteners, i.e. coca zero and coco light, demonstrating the ant's capacity to distinguish between real sugar and artificial sweeteners. Strikingly, both ant species preferred sugar containing coca cola to sugarwater. The invasive garden ant did not show preferences among four different types of sugary coke. But surprisingly, the Argentine ant preferred cherry coke over caffeine-free coke and vanilla coke, which she preferred over classic coke. The results demonstrated that the Argentine ant was able to discriminate among different coke flavours. In addition, she could distinguish between classic coke and caffeine-free coke, preferring the latter.

Limitations of our approach include the artificial lab set-up. Future field studies might test recruitment in areas where these species are invasive (parcs, picnic areas, roads). In addition, it would be interesting to test preferences of further soft drinks and perhaps sugary alcoholic drinks (such as fruity cocktails) or even food (good candidate substance seem to be ice cream, cookies, jam, bubble gum, bonbons). A further question that needs investigation is whether other invasive ant species have similar diet preferences.

Future research may also try to link behavioural responses to diets of different types of soft drinks or sugarwater. It is already known that ants fed on a high carbohydrate diet

display greater aggressiveness (Grover et al., 2007). It may be possible that ants fed on coca cola differ in their behaviour (e.g. even greater aggressiveness?)

Our study clearly demonstrates that it is too simplistic to state that invasive ants are attracted to 'sweet' substances. Their diet preferences appear to be more complex. This is highly relevant to field-based research. Usually baiting studies use different general types of food resources (protein, sugar, seeds) but do not discuss the choice of the bait (refs). In particular a variety of different baits, such as different brands of cookies or honey, are used, assuming that all ants with preferences for sweet substances are similarly attracted to different types of food. However, if this is not the case, this may introduce a bias in these studies. Here, I showed that cherry coke attracted more *L. humile*, while classic coke attracted more *L. neglectus*. That means that a field study using cherry coke as bait would have over-estimated the relative abundance of *L. humile* and under-estimated the relative abundance of *L. neglectus*. The reverse is true for normal coke. On the other hand, caffeine-free coke and vanilla coke seemed equally attractive to both species and would not introduce a bias if they were used as bait. This study highlights the importance of testing relative bait preferences of different species and/or their ability to detect them beforehand. In addition, knowing different diet preferences in invasive ants could have application in development of chemical treatments (Hoffmann and Saul, 2010).

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# Applied Ecology

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## APPLIED ECOLOGY

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Applied ecology aims to relate ecological concepts, theories, principles, models, and methods to the solving of environmental problems, including the management of natural resources, such as land, energy, food or biodiversity.

### DEFINITION AND SCOPE

#### What Is Applied Ecology?

Despite its somewhat restrictive name, applied ecology is more than simply the application of fundamental ecology. In a nutshell, ecological management requires prediction, and prediction requires theory. Applied ecology is a scientific field that studies how concepts, theories, models, or methods of fundamental ecology can be applied to solve environmental problems. It strives to find practical solutions to these problems by comparing plausible options and determining, in the widest sense, the best management options.

One particular feature of applied ecology is that it uses an ecological approach to help solve questions concerned with specific parts of the environment, i.e., it considers a whole system and aims to account for all its inputs, outputs, and connections. Of course, accounting for everything is no more possible in applied ecology than it is in fundamental ecology, but the ecosystem approach of applied ecology is both one of its characteristics and one of its strengths.

Indeed, one could view the overall objective of applied ecology as to maintain the focal system while altering either some of the elements we take from the system (i.e., ecosystem services or exploitable resources) or some of those we add to the system (i.e., exploitation regimes

or conservation measures) through an educated management strategy. Since those two types of elements are not mutually independent, long-term management strategies are best aimed at optimizing rather than maximizing exploited items. This is more efficiently achieved through an adequate understanding of theoretical ecology, which generally considers all parts of the system rather than a limited set of its components.

#### What Are the Fields Covered?

The word “applied” implies, directly or indirectly, human use or management of the environment and of its resources, either to preserve or restore them or to exploit them. Humans influence the Earth at all levels: the atmosphere, the hydrosphere (oceans and fresh water), the lithosphere (soil, land, and habitat), and the biosphere. Understandably, questions related to human populations (notably its demography) fall within the scope of applied ecology, as most impacts on ecosystems are directly or indirectly anthropogenic.

Aspects of applied ecology can be separated into two broad study categories: the outputs and the inputs (Fig. 1). The first contains all fields dealing with the use and management of the environment for its ecosystem services and exploitable resources. These can be very diverse and include energy (fossil fuel or renewable energies), water, or soil. They can also be biological resources—for their exploitation—from fish to forests, to pastures and farmland. They might also, on the contrary, be species we wish to control: agricultural pests and weeds, alien invasive species, pollutants, parasites, and diseases. Finally, they can be species and spaces we wish to protect or to restore.

The fields devoted to studying the outputs of applied ecology include agro-ecosystem management, rangeland management, wildlife management (including game), landscape use (including development planning of rural, woodland, urban, and peri-urban regions), disturbance management (including fires and floods), environmental engineering, environmental design, aquatic resources management (including fisheries), forest management, and so on. This category also includes the use of ecological knowledge to control unwanted species: biological invasions, management of pests and weeds (including biological control), and epidemiology.

The inputs to an applied ecology problem consist of any management strategies or human influences on the target ecosystem or its biodiversity. These include conservation biology, ecosystem restoration, protected area design and management, global change, ecotoxicology

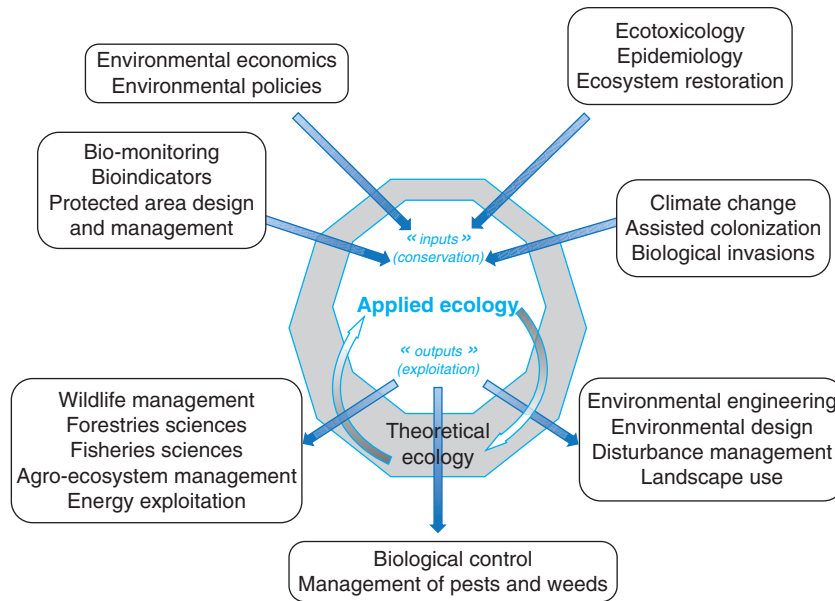


FIGURE 1 The relationships between the different fields of applied and theoretical ecology.

and environmental pollution, bio-monitoring and bio-indicators of environmental quality and biodiversity, environmental policies, and economics. Of course, these outputs and inputs are intimately connected. For example, the management of alien invasive species is relevant to both natural resource management (e.g., agriculture) and the protection of biodiversity (conservation/restoration biology).

In addition to using fundamental ecology to help solve practical environmental problems, applied ecology also aspires to facilitate resolutions by nonecologists, through a privileged dialogue with specialists of agriculture, engineering, education, law, policy, public health, rural and urban planning, natural resources management, and other disciplines for which the environment is a central axiom. Indeed, some of these disciplines are so influential on environmental management that they are viewed as inextricably interlinked. For example, conservation biology should really be named “conservation sciences” because it encompasses fields that are not very biological, such as environmental law, economics, administration and policy, philosophy and ethics, resources management, psychology, sociology, biotechnologies, and more generally, applied mathematics, physics, and chemistry.

And obviously, as we are dealing with environment and ecosystems, everything is connected, all questions are interrelated, all disciplines are linked, and all answers are interwoven. Understanding a process through one field of applied ecology will allow advancing knowledge in other fields.

### What Are the Links between Applied and Theoretical Ecology?

Because theoretical ecology may be defined as the use of models (in the widest sense) to explain patterns, suggest experiments, or make predictions in ecology, it is easy to see that relations between theoretical and applied ecology are bidirectional. Simply put, theory feeds application, but application also allows for the testing of theory. Indeed, applied ecological problems are used to assess and develop ecological theory. In this regard, these two aspects of ecology complement and stimulate each other.

Yet the links between theoretical and applied ecology can fray. Theoretical ecology operates within the bounds of plausibility. What is theoretically plausible, however, is not always ecologically realistic. And if it is not ecologically realistic, then theoretical ecology cannot be applied to interrogate real ecological situations. In other words, theoretical ecology cannot always be used in applied ecology. The links between theoretical and applied ecology range from spurious to robust and have been used with varying success in different fields. Fields that have benefited from theory include fisheries and forestry management and veterinary sciences and epidemiology (both human and nonhuman). However, some other fields of applied ecology have not (or not yet) benefited fully from ecological theories, concepts, and principles, and that aspect is the focus of this entry.

Three such examples are presented here. The first is an illustration of a major field of ecology that has a strong applied branch but has not, until very recently, fully

taken advantage of theoretical ecology: invasion biology. The second describes a theoretical process important to many aspects of applied ecology (including epidemiology, fisheries, biological control, conservation biology, and biological invasions) but which has nonetheless been underused so far in applied ecology: the Allee effect. The third depicts an emerging field that is now, by obligation, mostly theoretical but which has an applied future and for which it is hoped that ecological applications will emerge rapidly: climate change.

#### APPLIED ECOLOGY WITHOUT THEORETICAL ECOLOGY: BIOLOGICAL INVASIONS

The study of biological invasions is one striking case where applied ecology has historically been at the core of the discipline's development without fully benefiting from theoretical ecology. Alien invasive species are those species introduced beyond their ordinary geographical range by human agency and that are infamous for causing ecological and economical damage. Globally, they are considered as the second biggest cause of species extinctions after habitat degradation, but they reign as the single most devastating impact in island ecosystems.

The seventeenth century marked the start of the vigorous and uninterrupted human colonization of the world's islands, initially by sailors, pioneers, settlers, hunters and fishermen, and more recently by militaries and tourists. Whether by a poor understanding of ecosystem functioning or a scarce consideration for the environment, this colonization led to many ecological disturbances, in particular the introduction—deliberate or accidental—of many exotic plant and animal species. Although not confined to islands (exotic organisms have been introduced to continents, lakes, and even oceans), the introduction of exotic organisms to islands has often led to dramatic changes in their communities. This is in part because insular ecosystems are fragile and characterized by simple trophic webs, vacant ecological niches, and low species diversity. Perhaps more important, however, is the fact that native species often evolve in the absence of strong competition, herbivory, parasitism, or predation and are less adapted to these newcomers. Moreover, islands harbor high levels of endemism, several times higher than comparable continents ecosystems, which makes every population extirpation a probable species extinction. As a result, alien invasive species on islands have affected countless island plant and animal communities and have been responsible for numerous native species extirpations and extinctions (nearly 60% of modern species extinctions have occurred on islands).

The first attempts at controlling alien invasive species included mechanical (trapping, hunting) and chemical (poisoning) methods, but the majority were biological: deliberate introductions of the alien invasive species' natural enemies to efficiently find and kill them. For example, numerous attempts at controlling invasive rodents have involved releasing cats, dogs, or mongooses. Prior to many of these attempts, it had not been realized that even the most efficient predators very seldom remove an entire prey population but instead control it at reduced numbers. This is because invasive rodents have evolved with cat predation and have developed antipredator behaviors and high reproductive rates. Unfortunately for the native species that evolved in the absence of these predators and whose populations were impacted by them, this problem could have been anticipated since it is a fundamental prediction of predator–prey models and evolutionary ecology theory.

A famous example of such misguided attempts is the case of the repeated endeavors at controlling rodents in sugarcane fields in Jamaica during the nineteenth century. There, cane growers introduced ants (*Formica omnivora*), which did not reduce rat numbers but soon became a problem themselves. To remove rats and ants together, it was then decided to introduce toads (*Bufo marinus*). But toads still did not control rats, and they too became a pest themselves. Finally, small Indian mongooses were introduced to control rats and toads. Mongooses failed to control either and began preying on native birds, posing new threats to wildlife.

Another illustration of using biological methods in the absence of a careful theoretical framework is the use of pathogens to control invasive rabbits. The introduction of the myxoma virus into both Europe and Australia to reduce rabbit numbers, and the more recent introduction of rabbit haemorrhagic disease (RHD) into New Zealand for the same goal, were both designed without a proper ecological framework and performed neither by ecologists nor by conservation managers. These two cases point out how difficult it may be to fully control the intentional introduction of microorganisms by persons who are not fully aware of (and/or interested in) the potential ecological effects of such actions. Theoretical epidemiology was, however, sufficiently advanced to predict these unfortunate outcomes. Sadly, history now shows that the absence of a rigorous theoretical framework often renders these empirical attempts to apply simple ecological principles (e.g., predator–prey or host–parasite interactions) to real ecological problems prone to failure.

Unfortunately, early conservation managers, too, used trial and error to design island restoration projects, to the

point that the whole subdiscipline of alien invasive species control has been long dominated by empirical development of techniques and methods at the expense of the use of ecological theory. For example, chemical advances have led to powerful, specific poisons, and ingenious trapping devices have outwitted even the most cunning invasive mammals. But these are technological developments that do not rely much on theory. With the notable exception of Virus-Vectored immuno-Contraception, in which empirical and theoretical studies were developed in parallel, most of the progress made in this field has neglected the potential benefits of theoretical ecology. This understandably might have been because there was an urgent need for a specific application. Yet this general trend has also led to many delays (and even some failures) in eradication programs.

Recent advances to address failing eradication programs have spawned adaptive control programs. This second generation of control programs capitalizes on theory by using ecological concepts from population dynamics and behavioral ecology. Such theory has been used in a number of ways. For example, it has advised that the timing or order of species eradications can be used maximize their success, that techniques such as the “Judas goat” technique can exploit herding behavior to locate the last individuals, or that helicopters and GIS can be used to deliver baits more accurately. More recently, it has allowed us to develop a better understanding of spatial ecology in the first stages of rodent invasions on islands, in order to better detect and control them at this crucial step.

Despite the improvements in the second-generation adaptive control programs, they still often lack an ecosystem perspective, leading to a general underappreciation of the importance of chain reactions following sudden alien invasive species eradications. As, understandably, nongovernmental organizations, conservation managers, and wildlife bodies have to react faster than the rate at which fundamental research can operate, some eradication plans have suffered from a lack of pre-eradication studies aimed at understanding the direct and indirect biotic interactions linking native and alien invasive species. As a result, some exotic species that were held in low densities by alien invasive species exploded once the pressure from the alien invasive species was removed following their eradication, leading to further damage to the native ecosystem. For example, invasive goats were recently removed from the threatened native forest on Sarrigan Island, in the tropical western Pacific Ocean. Unfortunately, goats were selectively suppressing an exotic vine (*Operculina ventricosa*), which was highly competitive

compared to other native plants and eventually exploded following the release from goat browsing.

Although a few empirical examples exist, the study of these “surprise” secondary effects of alien invasive species eradications has been largely theoretical. Take, for example, the mesopredator release effect. In theory, when a native species is a shared prey of introduced predators (e.g., cats and rats), the removal of the introduced top predator (cat) might result in a numerical increase of the introduced mesopredator (rat) population. This increase may be highly detrimental for the native species. In this case, these biotic interactions were studied theoretically through a mathematical model, and there have been few empirical studies of this “surprise” effect. This situation seems to occur only under certain ecological circumstances (e.g., absence of alternative food resources) and depends on which species are affected. Similarly, the competitor release effect suggests that when controlling for a higher competitor (e.g., a rat), the population of the lower competitor (e.g., a mouse) may erupt, even if these are controlled at the same time. This is simply because under certain conditions the direct effect of the removal is lower than the indirect, positive effect of the competitor’s removal. In that case, the more severe the control, the more sudden the competitor release. This may explain why in several cases the eradication of rats was followed by a dramatic explosion of hitherto overlooked introduced mice.

Ideally, eradication programs should be based on a thorough knowledge of the interactions between the species involved, in particular regarding other introduced species. This principle has been applied to a long-term study that included removal invasive black rats from Surprise Island in the Entrecasteaux Reef, New Caledonia. Over a 4-year period, the island flora and fauna was characterized qualitatively and quantitatively to study the impact of rats on native species but also to reveal the presence of other introduced species: mice, ants, and plants. A thorough study of the trophic relationships within the invaded ecosystem, both empirical and theoretical (including mathematical modeling), led to the design of a case-specific eradication strategy that enabled removal of the rats without triggering a release of other invaders (e.g., simultaneous mouse removal was planned into the case-specific protocol). Then, this ecosystem has been the subject of a long-term post-eradication survey to follow both the recovery of the local communities and the potential emergence of surprise effects following the removal of rodents. This shows how theoretical ecology (here trophic ecology) may be helpful in improving the efficiency of applied ecology programs.

Because it is not possible to conduct long pre-eradication studies before each eradication control, as was done for Surprise Island, the establishment of robust control programs rooted deeply in theoretical ecology will be necessary to achieve the full potential of this central area of applied ecology.

#### THEORETICAL ECOLOGY WITHOUT APPLIED ECOLOGY: THE ALLEE EFFECT

In contrast to the case of biological invasions, population dynamics, and in particular the domains developing around the Allee effect, is a discipline deeply rooted in theoretical ecology, but it still lacks the full transfer to applied ecology.

A demographic Allee effect describes a reduced per capita population growth rate in a population reduced in size (or density). Theory suggests that many, or even most, species could be susceptible to a demographic Allee effect, either directly, or indirectly through interaction with another species. As a consequence of this perceived ubiquity, it has become a cornerstone concept of ecology, with many potential applications to population management. Since its origins in the 1940s, the Allee effect has been the subject of roughly two types of studies: those aiming at a better understanding of the mechanisms underpinning it and its theoretical implications, and those trying to assess the presence of this process in given taxonomic groups. Probably because the concept is intellectually exciting, but also because empirical and experimental approaches are generally more difficult, the theoretical line of study has been the most active.

Another reason for the dominance of theory-based studies in this field is that empirical demonstrations of Allee effects are scarce and have mostly been restricted to mechanisms affecting individual fitness (component Allee effects) rather than manifestations in population dynamics (demographic Allee effects). There are sound biological reasons why demographic Allee effects might be the exception rather than the rule, although these are irrelevant to the point made here. What matters is that the majority of Allee effect studies, particularly over the last decade, have been theoretical studies. Consequently, there is now a thorough understanding of the Allee effect based on its conditions, mechanisms, and implications in a variety of contexts, including single populations and metapopulations, interspecific interactions, and spatially explicit frameworks. The importance of this process for different fields of applied ecology, including conservation biology, species management, and population exploitation, is also well understood.

Yet studies on Allee effects conducted in the realm of applied ecology remain unfortunately scarce.

The fact is that managers and conservationists should be concerned about Allee effects, even in populations that are not apparently exhibiting them, because (i) they can create critical thresholds in size or density below which a population will crash to extinction, and (ii) even if there is no threshold, they increase extinction probability (due to stochasticity) and reduce per capita population growth rate in low-density or small populations. Whether extinction is a desirable or dreaded outcome, such knowledge may be critical for effective population management. For example, field studies of the spread of the wind-pollinated invasive cordgrass *Spartina alterniflora* in Willapa Bay, USA, reveal that it has been slowed by the existence of an Allee effect affecting plants in low-density areas, such as those that characterize the leading edge of the invasion, and this information has been central to control strategies.

Clearly, there is an important need for a whole line of work aimed at applying our theoretical understanding of Allee effects to solve real practical problems, particularly in those areas for which theory suggests it will have its greatest influence. One pressing situation that would deeply benefit from this transfer is the study of the conditions needed to maintain the population above the extinction threshold. This task will not be easy, especially since the extinction threshold is difficult to estimate and will vary according to both species and circumstance—habitat quality, mortality rates from predator or exploitation, and so on. But the benefits would likely be worth the effort. For example, it might be applied to invasion biology to enhance the efficiency of alien invasive species control programs. Theory states that targeting every individual of an introduced population might be unnecessary if the species exhibits a demographic Allee effect, with a substantial financial saving to be gained from leaving the last individuals to die out by themselves. Similarly, Allee effect theory can be used for the control of insect pests in agrosience. Several studies have investigated minimum propagule sizes for successful establishment of agents used in biological control programs.

Apart from management of introduced populations, Allee effect theory can also be used, somewhat obviously, in the management of threatened populations, affording managers an early warning system to avert their imminent extinction. For example, Allee effects interact synergistically with mortality from exploitation, which not only reduces the population size but can also create

or increase an extinction threshold. Exploitation of populations with possible Allee effects needs to be considered and managed very carefully. Examples of fishery collapses (and lack of recovery) show how the neglect of Allee effect theory in the implementation of maximum sustainable yields and quotas resulted in disaster. In 2006, Courchamp and colleagues showed that exploitation itself can also act as a mechanism to create an Allee effect, particularly if the economic value of a species is found to be increasing with rarity, and the implications of this new process remain to be studied. In addition to trying to preserve small and decreasing populations, it might be better to augment their size or distribution via translocation or population reinforcement. Just as Allee effects affect alien invasive species eradication campaigns, they will also alter reintroduction strategies. For example, reintroductions of quokkas and black-footed wallabies to Western Australia were met with failure because the sizes of the populations released were too small to overcome the sustained predation pressure from introduced cats and foxes.

Even studies of the second type, those aiming at finding an Allee effect in specific taxonomic groups, have suffered from a failure to use theory. It is now common knowledge that Allee effects may occur in a wide number of species and that the presence of this process may dramatically alter the conditions and chances of population viability. Yet entire taxonomic groups of conservation interest, including, for example, bats, primates, and felids, remain to be investigated in this context. Whether for conservation purposes or in relation to an economic interest, eusocial insects should also be a focus. For example, bees are of commercial importance and ants are of major relevance as biological invaders, and both are major providers of crucial ecosystem services. Yet these and the other tens of thousands of eusocial species of ecological importance have so far not been the subject of Allee effect studies (Fig. 2). Perhaps the only example of such a subject for an Allee effect study is a colonial spider (*Anelosimus eximius*), whose lifetime reproductive success (a composite measure of offspring production and survival) increases with colony size.

In many contexts, such as the study of alien invasive species, applied ecology has advanced through empirical studies despite the existence of a wealth of relevant theory. In other contexts, such as the study of Allee effects, theoretical ecology has been at the forefront of our understanding. Now, the time is right to use our theoretical understanding of processes such as the Allee effect to benefit applied ecology.



**FIGURE 2** Argentine ants (*Linepithema humile*), as an illustration of a species fitting the three examples detailed in this entry. They are one of the worst biological invaders in several parts of the world. In southern Europe, this species forms a supercolony from Spain to Italy and is likely to present an Allee effect. There, it seems unable to expand its range northward of its current area of invasion because of unsuitable climatic conditions at higher latitudes, but models predict that this is likely to change with global climate change. Photograph by Alex Wild.

#### THEORETICAL ECOLOGY FOR APPLIED ECOLOGY: CLIMATE CHANGE

A final example concerns an emerging area that has, up to now, mostly benefited from theoretical ecology, but which promises to be of major importance for future developments in applied ecology: climate change.

Over the last two centuries, anthropogenic activities have caused rapid climate change, with the mean global annual temperature expected to rise by 1–3.5 °C by 2050. Although climate change encompasses a wide range of phenomena like changes in precipitation regimes, increases in extreme event frequency, ocean acidification, and sea level rise, the vast majority of studies concern rises in temperature, which currently figures among the biggest threats to biodiversity. Species' responses to climate change have already been observed in many taxa. They include physiological changes, phenological changes (i.e., the timing of life cycle events such as plant flowering and fruiting or animal migration and reproduction), and geographic range shifts where species migrate to an area with a more favorable climate. If a species fails to adapt or to shift their ranges in response to climate change, then they may go extinct. This is the major prediction of many studies that have projected global biodiversity loss due to climate change. In one of the most widely cited studies, Chris Thomas and colleagues estimate that 15–37% of species are “committed” to extinction. It is clear that there is an urgent need to revise conservation strategies in

the face of global climate change, and because these predictions are based on events yet to pass, we must turn to the theory of climate change science to serve as the basis of these revisions. Because it is based on projections, the field of climate change biology has taken off by mainly developing a foundation of mathematical models that aims to predict species' potential ranges and fates under different scenarios.

There are two main categories of predictive models commonly used in climate change science. The first category represents the most widely used bioclimatic envelope models. They relate a current species' range to multiple environmental variables (such as temperature, precipitation, and so on) and thereby define the climatic niche of that species (its potential spatial distribution based on these variables), making the assumption that it reflects its ideal climatic conditions. Under different climate scenarios, the species' predicted future geographical distribution can be identified. Species whose predicted distribution will be no longer be within their climatic envelope are predicted to go extinct.

The second category of models is based on a species' physiology. For example, dynamic global vegetation models estimate plant biodiversity loss following climate-induced changes in geochemical cycles and CO<sub>2</sub> concentrations because of their physiological constraints. Physiology-based models that can be applied to animals include degree-day models, which estimate the number of days per year that the temperature is above a critical minimum temperature—the temperature below which the species cannot survive. These models are particularly useful for ectotherms.

These models can, of course, be complemented to some extent by experimental studies (based on increased temperature) or comparison with past data (some effects of global warming have been observable for the last several decades), but for now the major source of ecological knowledge comes from modeling. Yet the major interest for ecology in this domain will probably be in applied ecology. For example, bioclimatic models can help to reevaluate the current set of protected areas. They can help to identify climatic refuges and heterogeneous microclimatic conditions that may be important to save a species from extinction. Furthermore, models can help to prioritize protected regions. For example, islands that are less susceptible to sea-level rise should be favored both for protection and as refuges for threatened species. A widespread view is that an important strategy is to enhance landscape connectivity to enable species to move through a matrix of interconnected habitats in order to

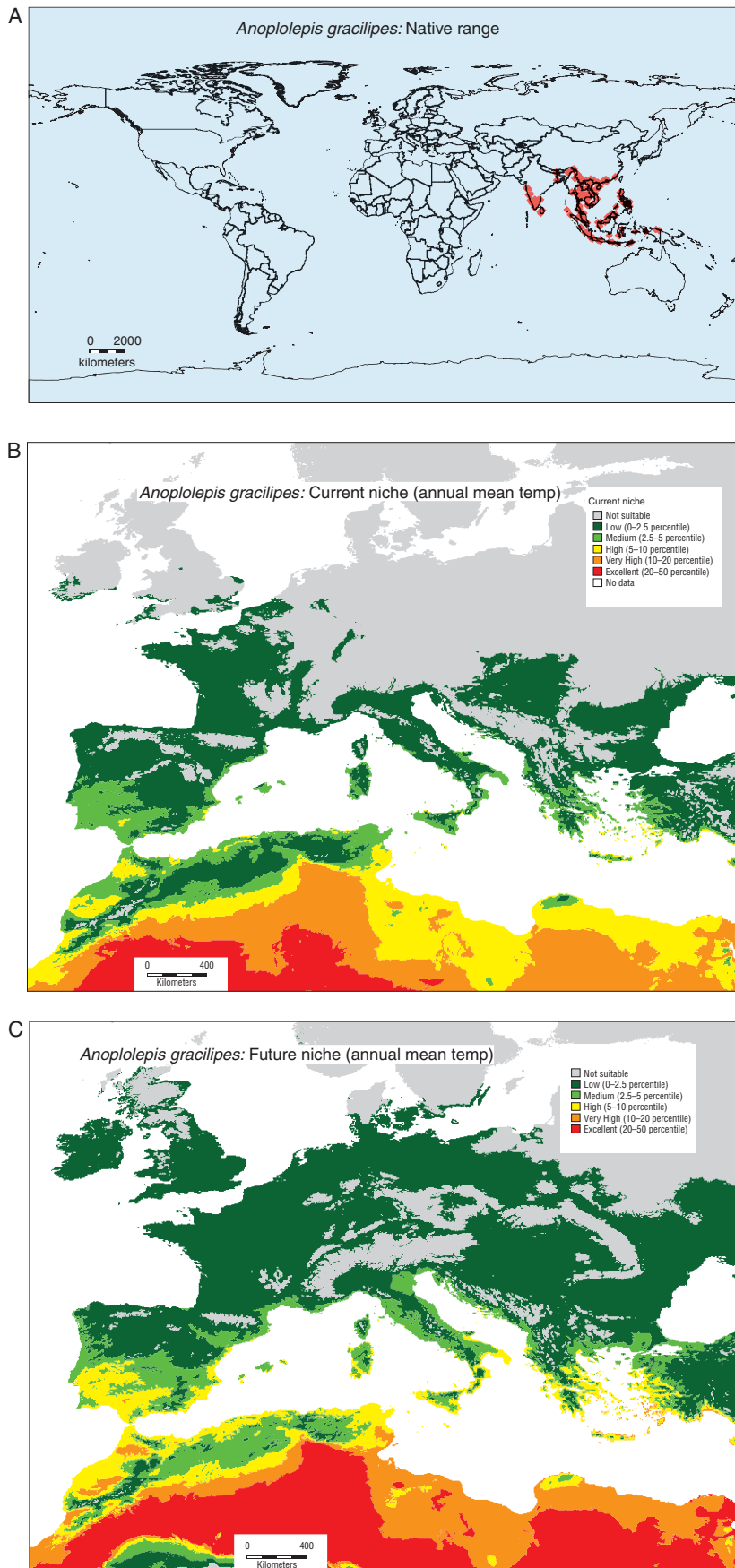
escape from unsuitable climatic conditions. However, as haunts the previous debates on corridors, enhancing landscape connectivity can also be argued as counterproductive because populations in the lagging edge of their advancing range would compete with arriving populations and communities. On the other hand, species range shifts might be the unavoidable consequence of climate change because a species' existing range might not overlap with its predicted future range. As this situation could lead to extinction, climate change has been a major argument for the proponents of human-assisted colonization. In this increasingly hot debate, it is likely that the solution might come from a solid blend of robust theoretical ecology and educated case-by-case decisions based on the known ecological characteristics of the concerned species and the socioeconomic context in which conservation is taking place. Surely theory has a major role to play here, too.

Bioclimatic models can also be used to explore the impact of different drivers of global change on biodiversity. For instance, it is very important to get a better understanding of how alien invasive species will react to climate change and whether they might benefit from shifting climatic envelopes to invade new areas previously outside their distribution. Models can help to identify species posing the greatest risk for invasion of a particular region under a scenario of climate change (Fig. 3).

Moreover, climatic models can also serve to evaluate the risks of disease spread following a rise in temperature, for example. Many disease vectors are very sensitive to climatic conditions, and there is a general fear that tropical diseases might extend to higher latitudes, leading to a dramatic increase of infectious diseases, especially when local hosts are naïve to the new parasites. This concerns plant, wild animal, domestic animal, and human populations.

These theoretical studies can help to estimate risks to biodiversity (invasions, diseases, species losses) and to prioritize protected areas. However, as all these projections of future biodiversity are based on models, they include the uncertainties inherent in their input variables, including projected climate change and the type of species' responses. They can thus be validated only indirectly, by extrapolating from observed changes over the last decades and through independent data sets of current species' occurrences. Even then, these models do not account for possible behavioral, phenological, or physiological adaptations and do not adopt an ecosystem perspective (communities will react differently than the sum of species





**FIGURE 3** Bioclimatic envelope models for the yellow crazy ant (*Anoplolepis gracilipes*) that relate the species' native distribution (A) to climatic variables (e.g., temperature) in order to determine the species' current climatic range that can then be projected on a climate map to determine its potential range based on climatic conditions in 2010 (B) and under a scenario of climate change, for example in 2050 (C).

reactions). Paradoxically, one may claim that the current theoretical approaches should be more closely based on theoretical ecology. Indeed, there is an urgent need to improve model predictions because many future conservation decisions will have to be made rapidly with the help of climate change model predictions.

Climate change science is, by its very nature, a predictive science, using today's concepts and models in developing a robust theoretical understanding of future climate change to advance the applied ecology of tomorrow.

### CONCLUSION: WHAT NOW?

This entry deals with the antithesis of theoretical ecology—applied ecology. A vast number of disciplines fall within its realm, and applied ecology provides theoretical ecology with a *raison d'être*. Applied ecology can (and should) benefit more from theoretical ecology, either by investigating new fields of applied ecology or by working to apply new concepts of theoretical ecology. This means not only that theoretical ecologists can look forward to a whole new set of questions, approaches, and tools to study, but also that they will have new subjects to explore and new colleagues to interact with.

The relationships between theoretical and applied ecology are better defined by a feedback loop than by a simple, unidirectional supply link. Enhancing the connections between these two complementary aspects of ecology will not only help solve pressing environmental issues but will also further stimulate theoretical ecology.

### SEE ALSO THE FOLLOWING ARTICLES

Allee Effects / Conservation Biology / Demography / Ecosystem Ecology / Fisheries Ecology / Invasion Biology / Restoration Ecology

### FURTHER READING

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## ASSEMBLY PROCESSES

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Ecological systems are dynamically nonlinear, self-organizing, spatially extended, and multistable, driven by species colonization and extinction events, all operating against a backdrop of environmental and spatial variation, disturbance, noise, and chance. System assembly or construction is fundamentally important to understanding ecological systems.

### ECOLOGICAL REALITIES

The nature of ecological systems creates a number of epistemological difficulties for the observer. When historical events have shaped the current system state, it becomes difficult for the observer to assign cause without knowledge of such events. For example, variation in the order of arrival and timing of species colonization has been shown to generate alternative community states. In fact, Drake, in 1990, found that assembling communities not only result in irrevocable differences in structure, but if perchance the developing trajectories cross (e.g., identical food webs), at some time they respond differently to a common invader. Such behavior is a consequence of both where each system came from and where they are going. This historical disconnect creates a very real danger when fundamental principles or cause are assigned based on our necessarily brief analyses of presently operating mechanisms, processes, and cycles. It is also unclear whether any given system is riding along a transient heading elsewhere or has reached some solution. This limits the power of experimentation to temporal slices of assembly time. How can the observer know whether the mechanisms and processes experimentally documented in a system are causal or are simply those permitted at a given time along some trajectory of development? Understanding these permissions is key to understanding biological nature. But how to proceed?



# Changements climatiques et biodiversité

Cleo Bertelsmeier



éléments de la biodiversité

# CHANGEMENTS ET

# CLIMAT BIOLOGIE

PAR CLÉO BERTELS

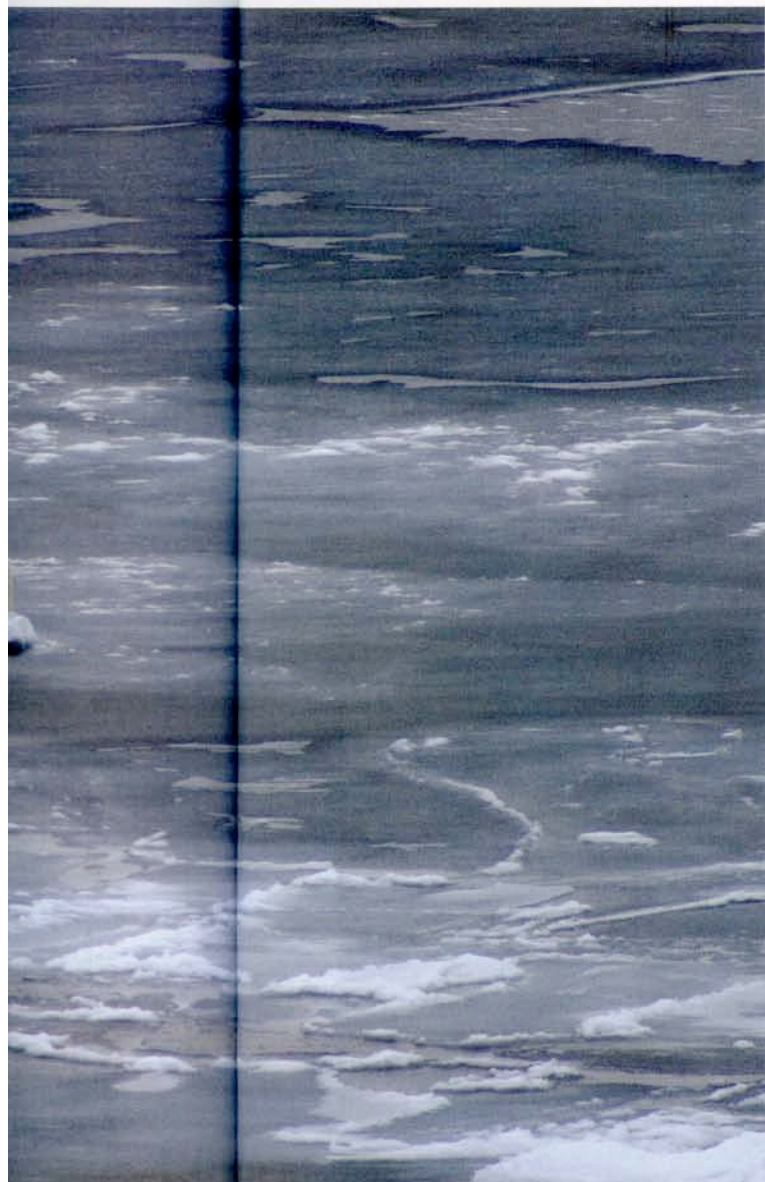


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# CLIMATIQUES BIODIVERSITÉ

PAR CLÉO BERTELSMEIER, DOCTORANTE EN BIOLOGIE À L'UNIVERSITÉ PARIS-SUD



Au cours de l'histoire, le climat de la Terre a changé en permanence, parfois rapidement, d'autres fois plus lentement, causant des extinctions d'espèces, des réarrangements de communautés ainsi que des modifications d'écosystèmes entiers.

Mais à l'heure actuelle, l'Homme est à l'origine d'un changement climatique rapide menaçant d'accélérer la perte de la biodiversité.

**S**elon les estimations, la température annuelle moyenne risque d'augmenter de 1 à 3,5 °C d'ici la fin du siècle. À titre de comparaison, pendant le dernier âge glaciaire il faisait en moyenne « seulement » 5 °C de moins par rapport à aujourd'hui. Il s'agit bien entendu de la moyenne sur la Terre entière et sur l'année. Or, les différences régionales seraient considérables : les hautes latitudes subiraient une hausse de température beaucoup plus prononcée que les tropiques. Cette augmentation de la température pourrait atteindre 8 °C en moyenne annuelle dans certaines régions du Canada. Mais le réchauffement pourrait être beaucoup plus important à certains moments de l'année. Outre un accroissement de température, le changement climatique inclut les précipitations (fig. 1), l'élévation du niveau de la mer, la réduction de la glace aux pôles (fig. 2), la fonte des glaciers et l'augmentation, en amplitude et en fréquence, des événements climatiques extrêmes (cyclones, ouragans, tempêtes...). Ces changements sont susceptibles de menacer une grande partie des espèces adaptées aux conditions climatiques de leur habitat, l'image emblématique traduisant cette menace







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Figure 2. Les icebergs et les banquises ont déjà commencé à fondre. Mais cet effet n'est pas linéaire. Moins il y aura de glace, plus elle fondra rapidement... © CNRS photothèque / Ipev / F. Delbart.



Figure 3. Les chercheurs commencent à comprendre les effets du changement climatique sur la physiologie, le comportement, la reproduction et la distribution des espèces, mais la très grande majorité des études s'intéresse seulement à une petite partie de la biodiversité, plus particulièrement aux animaux terrestres. Cependant, certaines estimations indiquent que deux tiers des espèces pourraient se trouver dans les océans, notamment la biodiversité « cryptique » (protistes, plancton...). Or, on connaît très peu de choses sur la biologie de ces organismes, et encore moins sur leurs réactions face au changement climatique. © CNRS photothèque / Tara océans / C. Sardet.

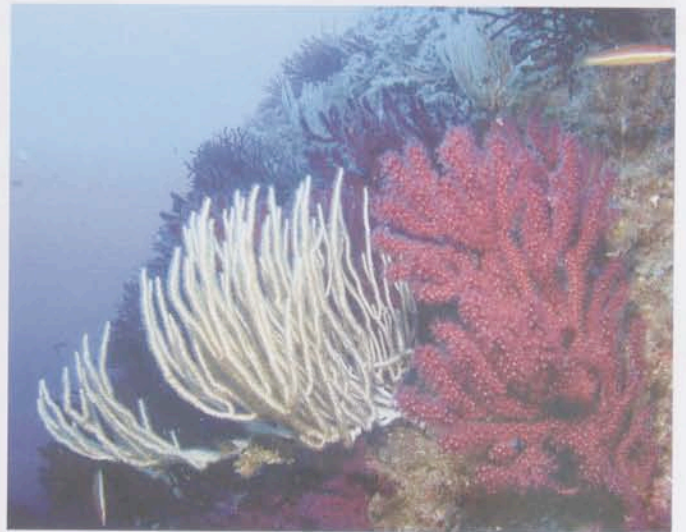


Figure 4. Les gorgones sont les éléments essentiels des paysages sous-marins de Méditerranée nord occidentale. Ce sont des espèces particulièrement sensibles au changement climatique global et notamment aux anomalies thermiques estivales. © CNRS photothèque / T. Perez.

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Même si, pour le moment, on a observé peu d'extinctions liées directement au changement climatique, de nombreuses études ont montré que les espèces y répondent déjà ; parmi elles, l'éléphant (fig. 5). Quelques exemples supplémentaires seront donnés par la suite.

#### ADAPTE-TOI... SI TU PEUX ! LA PHYSIOLOGIE MISE À L'ÉPREUVE

Confrontée à une hausse de température, une espèce pourrait s'adapter en modifiant sa physiologie. Ces changements concernent surtout une très grande majorité des espèces terrestres ectothermes (animaux « à sang froid ») comme les insectes, les reptiles et les

amphibiens, dont la physiologie est fortement dépendante du climat (fig. 6). Cela les rend très vulnérables au réchauffement climatique car certaines fonctions primordiales comme la locomotion, la croissance et la reproduction sont sensibles à de petites variations de température. De plus, chez beaucoup de reptiles la détermination du sexe des jeunes se fait pendant le développement dans l'œuf et dépend de la température. Chez de nombreuses tortues, par exemple, l'embryon aboutit à un mâle lorsque la température est inférieure à un certain seuil, et à une femelle s'il fait plus chaud. Ce phénomène peut s'observer pour un écart de

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Figure 5. Les conditions climatiques ont des effets sur la démographie des mammifères africains. Les éléphants du parc de Hwange, au Zimbabwe, l'un des parcs animaliers africains où la concentration animale est très importante, sont notamment sensibles à la sécheresse. Ici, ils se regroupent autour d'un trou d'eau où ils peuvent boire. © CNRS photothèque / S. Chamaille.

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température de seulement 1 à 2 °C. En raison du changement climatique, la proportion de l'un des deux sexes dans la population pourrait devenir trop importante... ce qui serait susceptible de menacer l'espèce.

Par ailleurs, la *fitness* (qui se mesure généralement par le nombre de descendants par individu) des animaux « à sang froid », comme les insectes, augmente progressivement avec la température et passe par un optimum. La température actuelle de l'habitat des insectes vivant dans des régions au climat tempéré est inférieure à leur température optimale (fig. 7). De ce fait, un réchauffement climatique pourrait avoir des effets bénéfiques sur la croissance de leur population. En revanche, les insectes tropicaux, comme la plupart des espèces, vivent dans des conditions proches de leur optimum thermique. Une faible augmentation de température pourrait les pousser en dehors de leur « zone de sécurité ».

Chez certaines espèces, la stratégie de reproduction dépend de la température. L'exemple des fourmis illustre parfaitement ce cas. Une jeune reine ailée peut essayer lors d'un « vol nuptial » et fonder une colonie toute seule après fécondation : c'est ce que l'on appelle la « fondation indépendante ». Une reine peut aussi quitter sa colonie en marchant, emportant avec elle un certain nombre d'ouvrières : c'est la « fondation dépendante ». Dans ce dernier cas, la nouvelle colonie s'implante à proximité de la colonie maternelle ; alors que dans le premier cas, la reine fondatrice peut voyager beaucoup plus loin. Chez certaines espèces de fourmis qui pratiquent les deux modes de fondation, les reines ailées sont nettement plus fréquentes à une température élevée. Ainsi, dans un scénario de réchauffement climatique, la colonie produirait davantage de reines ailées qui dispersent plus loin, ce qui permettrait à l'espèce de coloniser d'autres habitats plus rapidement. Il est possible que grâce à cette dispersion plus importante, la fourmi parvienne à



Figure 6. Les animaux « à sang froid » (poïkilothermes) comme cet iguane mexicain, *Ctenosaura pectinata*, sont particulièrement sensibles au changement climatique. La température a un impact non négligeable sur leur locomotion, leur physiologie et leur aire de distribution. © CNRS photothèque / E. Amice.

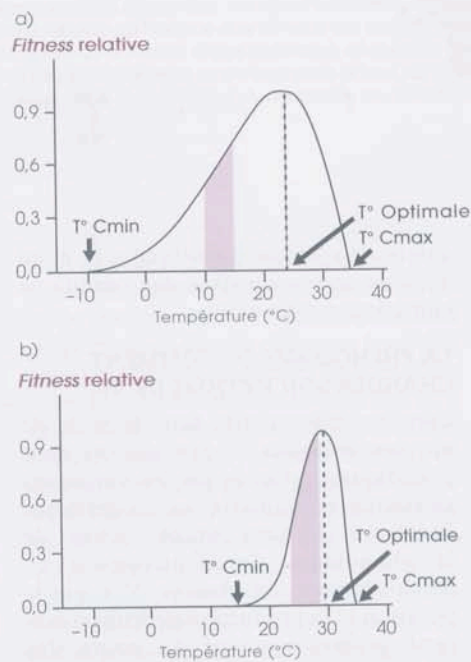


Figure 7. Les insectes qui vivent dans des zones tempérées (a) ont une tolérance thermique plus large que les insectes tropicaux (b). La zone colorée indique les températures actuelles de l'habitat des insectes. La courbe de *fitness* montre l'impact de la température sur les insectes. Une *fitness* nulle signifie que l'espèce est vouée à disparaître.

© M. Vergès, adaptation d'après Deutsch et al. (2008) PNAS.

*Linepithema humile* : distribution native

● *L. humile*



*Linepithema h*

Niche actuelle



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Figure 8. Un mod  
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suivre sa « niche climatique » et évite ainsi de se trouver dans des conditions climatiques défavorables.

**LA PHÉNOLOGIE OU COMMENT CHANGER SON RYTHME DE VIE**

Certains événements dans le cycle de vie des animaux et des plantes sont périodiques, rythmés par les variations saisonnières climatiques (migrations, floraisons...). Leur étude relève de la phénologie. Consécutivement au réchauffement, on observe déjà que la floraison et la production de fruits avancent progressivement au cours des décennies. Les migrations annuelles et la saison de reproduction suivent également cette tendance. Une étude de 143 exemples de changements phénologiques prenant en compte des espèces très variées – allant des mollusques aux mammifères, des herbes aux arbres –

a montré que 80 % des espèces ont avancé l'un des événements de leur cycle de vie dans l'année. En moyenne, toutes les espèces ont avancé leur reproduction de 5,1 jours tous les 10 ans depuis 50 ans, le record étant détenu par le guillemot de Troïl (*Uria aalge*) qui se reproduit 24 jours plus tôt par décennie. Plusieurs oiseaux en Europe et en Amérique du Nord migrent prématurément au printemps et les papillons apparaissent en moyenne 3 jours plus tôt en Grande-Bretagne. Même les marmottes anticipent leur sortie d'hibernation de 10 jours depuis 1970. Chez les plantes, les observations phénologiques incluent la date de floraison et l'émergence des feuilles, qui ont avancé de 1,4 à 3,1 jours par décennie. Certains chercheurs pensent que l'on risque de sous-estimer les conséquences du changement climatique en se focali-

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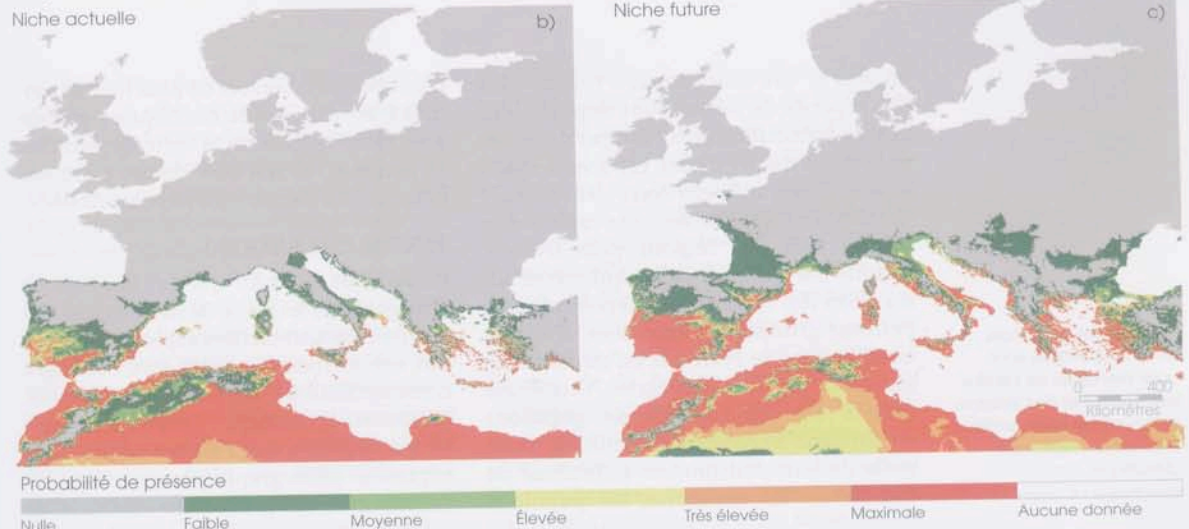
***Linepithema humile* : niche basée sur la température moyenne annuelle**

Figure 8. Un modèle de niche pour un insecte envahissant : la fourmi d'Argentine. Les chercheurs prennent une carte avec des points de distribution actuelle (a) pour trouver une relation entre la distribution de l'espèce et le climat à ces endroits (température, humidité...). Ensuite, on projette cette « niche » climatique sur une carte avec un climat actuel (b) et une carte avec un scénario de changement climatique (c). La comparaison des deux montre si l'habitat potentiel de l'espèce augmente ou diminue dans le futur. Ici, le résultat suggère que la fourmi d'Argentine pourrait envahir davantage d'endroits en Europe car le climat devient plus favorable. © C. Bertelsmeier.

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sant sur la réponse d'une espèce individuelle. Les espèces d'une seule communauté peuvent avoir des réponses différentes face au changement climatique. Si, par exemple, une plante fleurissait beaucoup plus tôt que son pollinisateur n'émerge, elle pourrait subir une diminution de son taux de pollinisation. De même, si un oiseau se reproduisait plus tôt mais que les ressources qui nourrissent les oisillons sont absentes, par exemple les chenilles, la reproduction risquerait alors d'être un échec.

#### FUYONS, ÇA CHAUFFE ! L'AIRE DE DISTRIBUTION... REDISTRIBUÉE

La distribution d'une espèce sur Terre est souvent déterminée par des conditions climatiques : une espèce ne peut pas coloniser des régions où il fait trop chaud, trop froid ou trop humide pour elle. Suite au réchauffement climatique, on devrait

pouvoir observer des redistributions d'espèces animales et végétales. Leur « enveloppe bioclimatique », l'ensemble des aires géographiques dont le climat est favorable pour l'espèce, va se décaler vers les pôles et vers les altitudes plus élevées (fig. 8). Il existe déjà un grand nombre d'observations d'espèces ayant modifié leur aire de distribution suite au changement climatique. Elles concernent surtout des espèces alpines et arctiques ainsi que les espèces qui peuvent migrer facilement comme les oiseaux, les invertébrés marins et les insectes. Une étude a montré que plus de 800 espèces appartenant à des groupes très divers – arbres, oiseaux, mammifères, poissons, amphibiens, insectes... – ont déjà changé leur aire de distribution. Les déplacements d'aire de répartition les plus importants se situent entre 200 km (des papillons) et 1 000 km (copépodes marins) rien que sur les quarante dernières



années ! En moyenne, toutes les 800 espèces de l'étude ont déplacé leur aire de distribution de 6,1 km par décennie et la majorité (65 %) des espèces a migré entre 35 et 240 km vers les pôles ! Certaines espèces ne sont pas capables de migrer vers des régions plus froides, comme par exemple celles qui vivent sur les pôles (fig. 9) ou en montagne : elles ne peuvent grimper indéfiniment, d'autant que l'habitat se restreint en raison de la forme en pic des montagnes. Une étude menée sur 16 espèces de papillons en Espagne suggère que l'altitude minimale de leur distribution a diminué de 120-200 m. En revanche, les papillons

n'ont pas pu coloniser de plus hautes altitudes, et leur aire de distribution globale s'est donc restreinte. Si cette déperdition se poursuit, 50 % à 80 % de ces papillons pourraient s'éteindre d'ici à la fin du siècle.

**RESTEZ CHEZ VOUS !**

Parfois, on voudrait que les espèces ne changent pas leur aire de distribution. Par exemple, de nombreuses espèces exotiques ont été introduites suite aux échanges commerciaux à travers toute la planète. Certaines deviennent « envahissantes », ce qui veut dire que l'espèce connaît une explosion démographique (en raison de l'absence de ses prédateurs habituels, de

Figure 9. Les manchots de la terre Adélie sont aussi menacés de perdre leur habitat et des sources de nourriture importantes suite au changement climatique. © CNRS photothèque / X. Crosta.



ses parasites qu'elle a une flore natives chassent des d'autres espèce adaptées aux pas se défend de croissance pas de dissim attaque pour tinction d'espèces importa qu'elles dispe des fleurs, ré autre espèce. entraîner des graves pour envahissante sont aujourd'I des principale sité. Le récha d'amplifier ce En effet, jusq introduites n' nouveaux te température de quelques « barrières th invasions bio

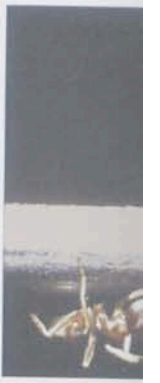


Figure 10. La men exacerbée par l'c invasives sont act pourraient s'établ Les conséquence

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Les espèces ne  
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aux échelles  
de toute la planète,  
des espèces  
« envahissantes »,  
qui ne connaissent  
pas ces barrières  
(en raison de  
leurs habitudes, de

de leurs parasites, de leurs compétiteurs...) et  
qu'elle a un effet néfaste sur la faune et la  
flore natives. Elles dévorent des plantes,  
chassent des proies, occupent les territoires  
d'autres espèces qui ne sont pas du tout  
adaptées aux nouveaux venus et ne savent  
pas se défendre (pas d'épines, de toxines ou  
de croissance accélérée pour les plantes ;  
pas de dissimulation, de fuite ou de contre-  
attaque pour les proies). Cela aboutit à l'ex-  
tinction d'espèces qui ont souvent des fonc-  
tions importantes pour l'écosystème parce  
qu'elles dispersent des graines, pollinisent  
des fleurs, régulent la population d'une  
autre espèce... Ainsi, leur disparition peut  
entraîner des conséquences écologiques  
graves pour l'écosystème. Les espèces  
envahissantes introduites par l'Homme  
sont aujourd'hui considérées comme l'une  
des principales menaces pour la biodiver-  
sité. Le réchauffement climatique risque  
d'amplifier cette menace !

En effet, jusqu'ici, beaucoup d'espèces  
introduites n'arrivaient pas à coloniser de  
nouveaux territoires en raison d'une  
température trop basse. L'augmentation  
de quelques degrés pourrait lever ces  
« barrières thermiques » et favoriser les  
invasions biologiques ! Par exemple, la

fourmi d'Argentine (*Linepithema humile*)  
a envahi une zone de plus de 6 000 km  
le long de la Méditerranée – du Portugal  
jusqu'en Italie (fig. 10). Ce faisant,  
la fourmi d'Argentine a déplacé de  
nombreuses espèces natives, infesté des  
maisons et détruit des cultures. Pour le  
moment, elle est fortement limitée à la  
région méditerranéenne. Cependant, des  
modélisations de l'évolution de sa « niche  
climatique » suggèrent qu'en cas de  
hausse de la température, la fourmi  
d'Argentine pourrait augmenter son aire  
de distribution au point d'atteindre peut-  
être l'Île-de-France. Il en va de même pour  
de nombreuses espèces envahissantes,  
parmi lesquelles les vecteurs de maladies  
dont on se préoccupe de plus en plus.

#### MALADIES ET PARASITES

De nombreux agents pathogènes sont  
sensibles à la température ou transportés  
par des vecteurs sensibles à la température,  
souvent des insectes. Par exemple, le palu-  
disme est transmis par des moustiques  
anophèles qui vivent dans des zones tropi-  
cales et pourraient étendre leur aire de  
distribution suite à un accroissement de  
température. On admet en général que le



Figure 10. La menace pesant sur la biodiversité à cause du changement climatique pourrait être exacerbée par l'arrivée d'espèces envahissantes, telles que la fourmi d'Argentine. Certaines espèces invasives sont actuellement limitées à des aires de distribution avec un climat plus chaud, mais pourraient s'établir à des latitudes plus élevées suite aux bouleversements climatiques. Les conséquences pour les espèces natives pourraient être dramatiques. © CNRS photographique / G. Theraulaz.



nombre de nouveaux pathogènes va augmenter avec le réchauffement climatique. Ainsi, le virus West Nile (ou virus de la fièvre du Nil occidental), transmis par des moustiques du genre *Culex* et des oiseaux migrateurs (comme deuxième hôte), est actuellement présent dans le Bassin méditerranéen où il est à l'origine d'épidémies de méningo-encéphalites parfois mortelles pour l'Homme. Suite à une augmentation de la température, on craint que les oiseaux ne modifient la durée ainsi que le trajet de leurs migrations et n'atteignent le nord de la France, par exemple, où le virus pourrait peut-être se propager. Par ailleurs, les espèces mobiles pourraient souffrir d'une augmentation de maladies transmissibles : les animaux qui changent leur route de migration en réponse au réchauffement climatique risquent d'entrer en contact avec des pathogènes auxquels ils n'ont jamais été exposés auparavant. Cette nouvelle maladie peut donc se révéler très vite fatale pour l'espèce car elle n'est pas dotée des défenses appropriées pour éliminer le pathogène. Cela a déjà été observé chez des phoques de la Mer du Nord qui ont rencontré le *phocine distemper virus* (virus de la maladie de Carré du phoque) après avoir changé leurs habitudes de migration...

Un point positif cependant : un certain nombre de maladies, que l'on croyait dépendre du changement climatique, ne semblent finalement pas être influencées uniquement par une augmentation de température. Par exemple, on redoutait qu'une forme de dengue, qui s'accompagne d'une fièvre hémorragique chez l'Homme, ne se répande plus rapidement. Mais de récentes études suggèrent qu'il n'en est rien et qu'il y aurait d'autres

facteurs plus importants qui détermineraient la transmission de cette maladie. De même, l'extinction de 67 % des amphibiens endémiques des tropiques américains est causée par un champignon qui se serait répandu de manière explosive après une augmentation de la température, selon une étude très citée. Toutefois, il apparaît depuis peu que la transmission du champignon est également dépendante d'autres facteurs, comme la formation de brouillards et la pollution accrue en aérosols. Pour le moment, il n'est pas évident que le réchauffement climatique soit le facteur décisif dans l'extinction catastrophique des grenouilles.

#### UN PEU DE LUMIÈRE À L'HORIZON...

Même si certaines projections des modèles bioclimatiques prédisent une perte de 15 à 37 % de toutes les espèces sur Terre avant 2050, tout n'est pas noir ! En fait, le changement climatique pourrait aussi avoir des effets bénéfiques sur la biodiversité. Un certain nombre d'espèces, notamment de plantes, pourraient bénéficier de températures plus clémentes en hiver ou favoriser leur croissance grâce à l'augmentation du  $\text{CO}_2$  dans l'atmosphère (fig. 11). Par ailleurs, le réchauffement climatique ne sera pas homogène partout au monde.

Figure 11. Mesures au large de l'île de Batz, dans le Finistère, pour étudier le flux de carbone. Dans un contexte d'augmentation de la concentration de  $\text{CO}_2$  dans l'eau de mer, ces mesures permettent d'en apprécier la quantité qui pourra être assimilée par des systèmes côtiers particuliers soumis au changement climatique.

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Une étude prédit par exemple l'expansion des mangroves dans certaines régions. Ensuite, il a été observé que certaines espèces envahissantes et plusieurs maladies pourraient suivre la tendance globale et donc s'éteindre (du moins localement), ce qui est plutôt une bonne nouvelle. Certains chercheurs pensent que le changement climatique pourrait affecter l'aire de distribution potentielle des pathogènes et de leurs

hôtes de manière différente ! Cela pourrait rompre la relation hôte-parasite et conduire à l'extinction du parasite... En dépit de cette petite note positive, n'oublions pas qu'une grande partie de la diversité de la vie sur Terre pourrait disparaître d'ici à la fin du siècle. Le changement climatique est ainsi l'un des plus grands défis pour les biologistes qui œuvrent pour la conservation des espèces ! C'est un débat de grande

Figure 12. Les forêts tropicales sont l'habitat d'un nombre incroyable d'espèces. On pense qu'environ trois quarts des animaux et des plantes terrestres vivent dans ces forêts. De plus, elles absorbent une grande partie du CO<sub>2</sub> émis par les activités humaines. À l'heure actuelle, ces forêts sont doublement menacées : d'une part par la déforestation et d'autre part par le changement climatique qui risque d'assécher certaines forêts et d'augmenter la fréquence des feux de forêt. © CNRS photothèque / C. Delhay.



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actualité : comment adapter des stratégies de protection des espèces en tenant compte du réchauffement climatique ? L'une des propositions est de faciliter les changements d'aire de distribution des espèces en créant des « corridors » de milieux naturels connectés qui permettraient aux espèces de migrer librement. L'inconvénient est que cela pourrait faciliter les invasions biologiques aussi. Certains écologues proposent même de transporter des espèces menacées dans un autre habitat pour les sauver de l'effet du changement climatique. Mais il y a une forte opposition à cette idée car une telle introduction peut avoir de nombreux risques imprévus pour la faune et la flore natives, les espèces introduites pouvant devenir envahissantes.

Un point sur lequel les écologues semblent être d'accord est qu'il va falloir revoir le choix des réserves naturelles pour ne pas dépenser beaucoup de ressources en la protection d'une île, par exemple, sur laquelle les espèces endémiques vont probablement s'éteindre faute de possibilités de migrer ailleurs. Développer de nouvelles stratégies de conservation est urgent car la plupart des espèces vont être affectées par le changement climatique, soit directement par des effets sur leur physiologie, leur phénologie ou leur aire de distribu-

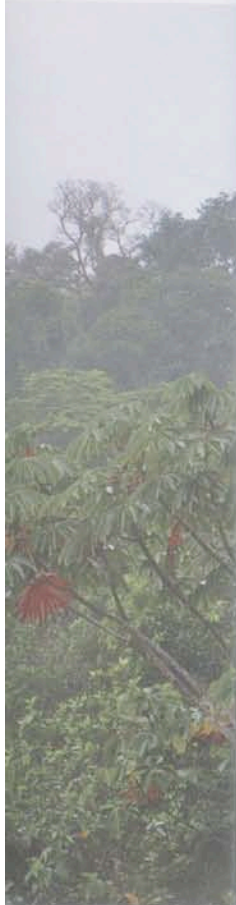
tion, soit indirectement par « effet domino » à travers une relation symbiotique, mutualiste, d'hôte/parasite, de prédateur/proie ou de compétiteur.

À l'heure actuelle, les chercheurs sont en train d'améliorer leurs modèles mathématiques pour pouvoir prédire la perte de la biodiversité vers la fin du siècle. Toutes ces projections doivent s'appuyer sur un certain nombre de suppositions concernant le scénario de développement humain, l'augmentation exacte de la température, la capacité des espèces à s'adapter, leur tolérance physiologique et l'interaction du changement climatique avec d'autres menaces de la biodiversité (fig. 12)... Par conséquent, les chiffres des espèces « vouées à l'extinction » varient considérablement. Mais une chose est claire : même si l'on ne sait pas (encore ?) prédire la perte de la biodiversité avec une grande certitude, les chercheurs s'accordent tous sur le fait qu'un grand nombre d'espèces va être affecté par le changement climatique et va s'éteindre. La certitude des chercheurs selon laquelle c'est bien le réchauffement climatique qui est déjà à l'origine de réponses physiologiques, phénologiques et de changements d'aire de distribution réside surtout dans le nombre d'observations faites sur des milliers d'espèces dans tous les écosystèmes et leur variété. C. B.

### Cléo Bertelsmeier

**Cléo Bertelsmeier est doctorante à l'université Paris-Sud.**

Son sujet de thèse porte sur l'impact du changement climatique sur les invasions de fourmis. Elle effectue en parallèle un monitorat au Palais de la découverte.



## Summary

Climate change and biological invasions are both among the greatest threats to biodiversity and their impacts might increase by the end of the century. Among invasive species, ants are a prominent group due to their negative impacts on native species, ecosystem processes, human and animal health, agro-ecosystems and the economy. The objective of this thesis was to forecast future ant invasions – especially in the light of on-going climate change, which is generally thought to favour invasive species by removing thermal barriers. I used three complementary approaches to study the potential of different ant species to invade in the future: species distribution modelling, behavioural experiments and the analysis of a database of ecological traits.

I modelled suitable area for 15 of the worst invasive ant species, both currently and with predicted climate change, globally, regionally and within the world's 34 biodiversity hotspots. Surprisingly, the potential distribution of only five species was predicted to increase (up to 35.8%) with climate change, with most declining by up to 63.3%. The ant invasion hotspots are predominantly in tropical and subtropical regions of South America, Africa, Asia and Oceanic islands, and particularly correspond with biodiversity hotspots. Contrary to general expectations, climate change and biological invasions will not systematically act synergistically for ants. In addition, I found that the impacts of climate change can change over time and even reverse the trend of the impact (*i.e.*, an increase instead of a decrease or vice versa). However, ant invasions will likely remain as a major global problem, especially where invasion hotspots coincide with biodiversity hotspots.

The species distribution models have identified large potentially overlapping distributions of several invasive ants. In the future, these species may arrive simultaneously in the same regions and compete with each other. In a series of experiments, I tested behavioural differences among 7 highly invasive ant species (*Anoplolepis gracilipes*, *Paratrechina longicornis*, *Myrmica rubra*, *Linepithema humile*, *Lasius neglectus*, *Wasmannia auropunctata* and *Pheidole megacephala*). I discovered two different behavioural strategies among invasive ants. Interactions at the colony level, exhibited more complex demographic processes and more variability. Further, I investigated resource competition and differences in resource exploitation. I found significant differences among species, with competitive abilities that were negatively correlated with behavioural dominance. This series of experiments suggests that the 'mechanisms' of invasiveness are more complex than previously thought and that different invasive ant species may use different behavioural strategies.

Since there are more than 250 exotic species of ants, it would be interesting to identify potential future invaders. In order to identify traits associated with invasiveness in ants, I set up a database with 2193 ant species and 24 ecological characteristics. I performed a preliminary analysis of trait differences between native and invasive ants that shows clearly different clusters of invasive and native species, with exotic species in between. These results could be used as a basis to construct a predictive model of future ant invasions.

The different methods used (models, experiments, database) are complementary in that they explore different aspects of the future ant invasions which are likely to be influenced by on-going climate change. The worst invaders of tomorrow may not be the same as today and similarly, areas most at risk are likely to change.

Le changement climatique et les invasions biologiques comptent parmi les plus grandes menaces pour la biodiversité et leurs impacts pourraient augmenter d'ici la fin du siècle. Parmi les espèces envahissantes, les fourmis sont un groupe particulièrement néfaste du fait de leurs impacts sur les espèces natives, les processus écosystémiques, la santé, l'agriculture et l'économie. L'objectif de cette thèse était de prédire les invasions de fourmis – en particulier avec le changement climatique, qui pourrait favoriser les invasions en levant des barrières thermiques. J'ai utilisé trois approches complémentaires afin d'étudier le potentiel d'invasion de différentes espèces : des modèles de distribution, des expériences comportementales et l'analyse d'une base de données de traits écologiques.

J'ai modélisé l'aire favorable pour 15 espèces de fourmis parmi les pires envahissantes, à la fois globalement, par continents, et dans les 34 hotspots de biodiversité. La distribution potentielle de seulement cinq espèces est prédite pour augmenter (jusqu'à 35.8%) avec le changement climatique et l'aire potentielle diminue pour la plupart des espèces, jusqu'à 63.2%. Les hotspots d'invasions de fourmis se situent surtout dans des régions tropicales et subtropicales, notamment en Amérique du Sud, en Afrique, en Asie et sur les îles océaniques, qui correspondent largement aux hotspots de biodiversité. Contrairement à ce qui est généralement admis, le changement climatique et les invasions biologiques n'agiront donc pas de manière synergique, au moins pour les fourmis. Par ailleurs, j'ai trouvé que les impacts du changement climatique changent avec le temps et peuvent même inverser la tendance de l'impact (d'une augmentation à une diminution, ou inversement). Par contre, les invasions de fourmis resteront probablement un problème global majeur, en particuliers dans les zones où les hotspots de biodiversité et les hotspots d'invasion se superposent.

Les modèles de distribution ont identifié de larges zones de recouvrement entre aires favorables de plusieurs espèces de fourmis envahissantes. Dans le futur, ces espèces pourraient donc arriver dans les mêmes régions et entrer en compétition. Dans une série d'expériences au laboratoire, j'ai testé la compétitivité de 7 espèces de fourmis envahissantes (*Anoplolepis gracilipes*, *Paratrechina longicornis*, *Myrmica rubra*, *Linepithema humile*, *Lasius neglectus*, *Wasmannia auropunctata* et *Pheidole megacephala*). J'ai découvert deux stratégies comportementales différentes pour la compétition d'interférence entre petits groupes d'ouvrières. Les interactions au niveau de la colonie ont suivi des processus démographiques plus complexes. De plus, j'ai mis au point deux expériences pour tester la capacité des fourmis envahissantes à explorer un nouvel espace et à exploiter des ressources. J'ai trouvé des différences significatives entre espèces et leur capacité à dominer par interférence comportementale était négativement corrélée à leurs capacités à découvrir et exploiter des ressources. Cette série d'expériences suggère que les 'mécanismes' d'invasion sont plus complexes que ce qui est généralement suggéré et que différentes espèces pourraient utiliser des stratégies comportementales différentes.

Etant donné qu'il existe plus de 250 espèces de fourmis exotiques, il serait intéressant de pouvoir identifier à l'avance des envahisseurs potentiels. Afin d'identifier des traits associés au caractère envahissant des fourmis, j'ai mis en place une base de données qui contient 2193 espèces de fourmis et 24 traits écologiques. J'ai effectué une analyse préliminaire de différences de traits entre fourmis natives et envahissantes, qui a montré qu'il existe clairement des groupements distincts de natives et envahissantes, les espèces exotiques ayant des caractéristiques intermédiaires. Ces résultats pourraient servir de base pour construire un modèle prédictif des invasions de fourmis.

Ces différentes approches (modèles, expériences, base de données) sont complémentaires car elles s'intéressent à des aspects différents du futur des invasions de fourmis, qui sera vraisemblablement fortement influencé par le changement climatique. Le pires envahisseurs de demain ne seront probablement pas les mêmes qu'aujourd'hui et les zones les plus à risque pourraient changer également, mais les fourmis envahissantes resteront un problème majeur.