

## Invasions of ants (Hymenoptera: Formicidae) in light of global climate change

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### Abstract

Climate change and biological invasions are among the greatest threats to biodiversity, and their impacts might increase by the end of this 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. Ants are expected to be particularly sensitive to climate change. In this review, we examine the mechanisms by which climate change will affect future ant invasions and whether their interaction could lead to a synergistic effect. We describe three major modelling approaches used to forecast the future of invasions under climate change: species distribution models, mechanistic models, and coupled models, which couple range predictions with dispersal or population dynamics. We then examine predictions for invasive ant species globally, regionally, and within the world's biodiversity hotspots. These predictions are heterogeneous, varying in the magnitude and the direction of the impacts across species and across spatial and temporal scales. Overall, it is unlikely that climate change will systematically increase ant invasions. However, several invasive ants will benefit from more and higher climatic suitability and will therefore have the potential for further spread. Globally, spatial range predictions of future ant invasions will allow comparing and prioritizing the management of certain species and areas. Future development of invasion forecasts under climate change should particularly (a) focus on methodological improvements of the existing methods to qualitatively improve range predictions by incorporating the biotic interactions and microclimatic conditions experienced by ants, (b) tease apart the impacts of climate change on different stages of the invasion process, and (c) account for the combined impacts of changes in habitat disturbance and climate change on invasions.

**Key words:** Ant species, biological invasions, climate change, impacts, predictions, models, review.

Myrmecol. News 22: 25-42 (online 24 October 2015)

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 11 March 2015; revision received 28 July 2015; accepted 31 July 2015

Subject Editor: Nicholas J. Gotelli

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### Introduction

Global biodiversity is currently facing a crisis that has been called the sixth mass extinction in the history of the earth (BARNOSKY & al. 2011). 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 (VIÉ & al. 2008). The current biodiversity crisis has multiple causes linked to human activities. Species invasions and climate change are recognized as important causes of current and future extinctions (CLAVERO & GARCÍA-BERTHOUS 2005, BELLARD & al. 2012, SIMBERLOFF & al. 2013). These drivers of species extinctions do not act in isolation, and in fact, the greatest threat could stem from synergies between different drivers (BROOK & al. 2008, BELLARD & al. 2013). Here, we will examine the impact of climate change on biological invasions.

Determining how organisms respond to ongoing anthropogenic climate change and what conservation actions

should be taken to control for species invasion are among the most significant challenges in biology today. Climate change will not only affect the mean global temperature, projected to rise by 1.7 to 4.8 °C by the end of the century (IPCC, 2014), but also the extremes, namely, variability and seasonality. It is very likely that heat waves will occur with a higher frequency and with longer duration (IPCC, 2014). Climate change will also modify the patterns and variability of rainfall and change the frequency of extreme events such as floods, droughts, storms, and fires. Such environmental changes will affect all levels of biodiversity, from single organisms to whole biomes. 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 (BELLARD & al. 2012).

Shifts in phenology and distribution in response to climate change vary in both direction and magnitude among

species (SUNDAY & al. 2012). Tropical ectotherms are, for example, prone to suffer declines in mean fitness (DEUTSCH & al. 2008, DIAMOND & al. 2012), while at latitudes higher than 40°, climate change generally increases mean fitness (KINGSOLVER & al. 2013). This is because tropical species are living close to their optimal temperature and are thus more sensitive to warming than species living in cooler climates, which are further from their physiological warming tolerance limit (DEUTSCH & al. 2008, DIAMOND & al. 2012). Ectotherms are considered particularly vulnerable to climate change (SHELDON & al. 2011, PAAIJMANS & al. 2013). They are the predominant group of terrestrial animal species that either comply with their environment or rely on behavioural thermoregulation for optimum performance, fitness maximization, and survival (ANGILLETTA 2009, SUNDAY & al. 2014). Ectothermic organisms, such as insects, are of particular interest in this context. Both their larval development and adult activities are strongly sensitive to climatic conditions. The redistribution of species may, therefore, be one of the most significant responses of insects to climate change. In this context, it is generally assumed that most insect species should benefit from warmer climates to establish and spread outside their native range (HELLMANN & al. 2008).

The view that climate change will exacerbate invasions has become a widespread view in global change biology (e.g., DUKES & MOONEY 1999, SALA & al. 2000, BROOK & al. 2008). Climate change may increase biological invasions because the distribution of many invasive species is currently restricted by thermal barriers (too low temperatures), and climate change could enable them to invade higher latitudes (DUKES & MOONEY 1999, BROOK & al. 2008, HELLMANN & al. 2008).

In this review, we synthesize the literature on biological invasions within the context of global climate change. Our focus is on ants, a group that is both very sensitive to climate change and that counts among the worst invasive species worldwide. Ants are present on all continents except Antarctica at a wide range of latitudes, and their distributions are strongly affected by climate (SANDERS & al. 2007, JENKINS & al. 2011, ROURA-PASCUAL & al. 2011). In addition, exotic ant species (which are introduced by humans outside their native range) and, in particular, invasive species (exotic species that spread and cause environmental or economic impacts), constitute a relatively homogenous group sharing many ecological traits, such as polygyny, unicoloniality and omnivory (PASSERA 1994, HOLWAY & al. 2002). Therefore, they are an interesting taxonomic group for testing the effects of climate change on biological invasions. In addition, invasive ants are often considered among the worst of invasive species, for several reasons.

Ants are easily transported by humans because of their small size and generalist nesting habits. Many species nest in superficial or ephemeral sites such as root masses, leaf litter, logs and plant debris (SUAREZ & al. 2009). Exotic ants, which are intercepted at ports of entry (MCGLYNN 1999, LESTER 2005, SUAREZ & al. 2005, WARD & al. 2006), are frequently detected on plant material (SUAREZ & al. 2005). In total, more than 200 species have established populations outside their native range (SUAREZ & al. 2009), but it has been estimated that more than 600 species have already been introduced outside their native range (MIRA-

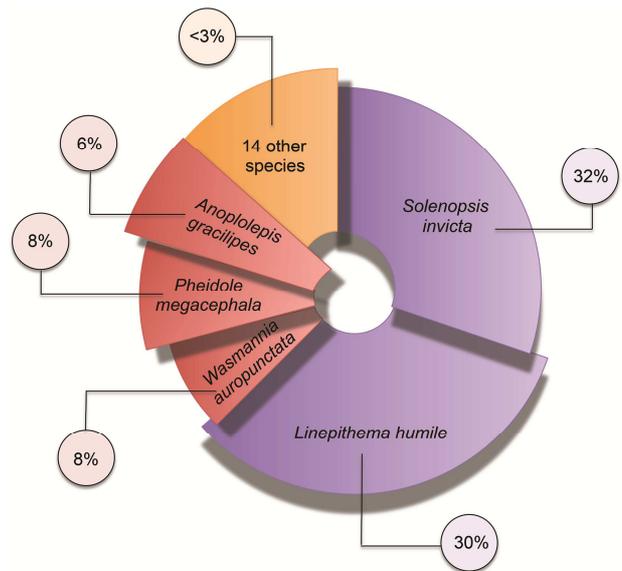


Fig. 1: Pie chart of the studies on 19 invasive ant species in the literature, showing a strong bias towards two species in particular (*Linepithema humile* and *Solenopsis invicta*, in purple), while three others amount to less than a quarter of the studies (in red). The 14 remaining all have less than 3% of the studies (in orange). Research in March 2015 in Web of Science, using "(invasi\* OR alien) AND (genus species)".

VETE & al. 2014). 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 (HOLWAY & al. 2002, LACH & HOOPER-BUI 2009, RABITSCH 2011). Currently, the IUCN Invasive Species Specialist Group (IUCN SSC INVASIVE SPECIES SPECIALIST GROUP 2012) recognizes 19 ant species as highly problematic, and five species are even on the "100 of the world's worst invasive alien species" list (LOWE & al. 2000): 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*). To date, very few studies are available on invasive species biology and ecology other than *L. humile* and *S. invicta* (Fig. 1).

Invasive ants are prominent among invasive species because of their enormous impacts on native biodiversity (Fig. 2). They reduce native ant diversity (WITTMAN 2014), displace other arthropods, and negatively affect many vertebrate populations (LACH & HOOPER-BUI 2010). This leads to impacts on ecosystem function, e.g., seed dispersal (LACH 2003) and soil chemistry (LACH & HOOPER-BUI 2009, STANLEY & WARD 2012). In addition, invasive ants can damage electrical equipment, invade buildings, and sometimes sting and cause anaphylactic shock, which can be fatal, and they can transmit diseases (MOREIRA & al. 2005, IUCN SSC INVASIVE SPECIES SPECIALIST GROUP 2012). In addition, they may be a nuisance in agricultural areas and reduce production (WIELGOSS & al. 2014). Overall, invasive ants can be economically costly (PIMENTEL & al. 2005, GUTRICH & al. 2007). Because ants are extremely difficult to control once they have invaded an extensive area, it is preferable to prevent ant invasions or to eradi-

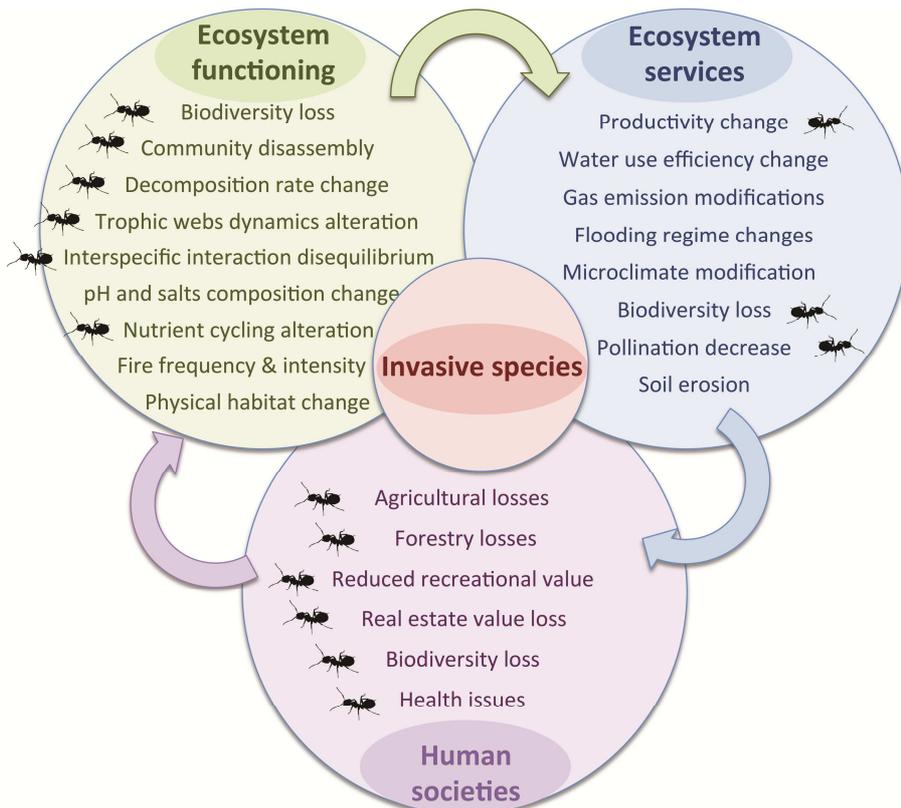


Fig. 2: Impacts of invasive species on ecosystem functioning, ecosystem services and human societies. The icon (ant) denotes when this impact has been documented in invasive ants.

cate the population when it is still relatively small (HOFFMANN & al. 2009). Forecasting potential ant invasions and understanding the impact of climate change on their distributional limits is important in this context, as it might allow prioritizing certain species or certain areas.

So far, no climate-change-induced ant invasions have been documented. However, this missing evidence does not exclude that past climate change has already had an impact on ant invasions over the last century. Current levels of climate change have already affected local ant assemblages, as has been shown in the south-eastern US (MENKE & al. 2014, RESASCO & al. 2014). Studies documenting invasion histories and introduction dynamics using genetic markers (SHOEMAKER & al. 2006, FOUCAUD & al. 2010, VOGEL & al. 2010, ASCUNCE & al. 2011) cannot attribute the invasion to changes in environmental conditions. However, it is possible that past climate change has driven recent invasions, but it is difficult to separate it from other confounding variables, such as increased introduction frequency or changes in land use. This is similar to the problem of assigning a single driver of species loss to the extinction of a given species, which is often impossible (SODHI & al. 2008). However, two native ant species have already been documented to shift their range to higher elevations following past climate change over a period of 38 years (WARREN & CHICK 2013), and invasive ants could follow the same pattern.

In this review, we will (I) examine the mechanisms by which climate change might influence future ant invasions, (II) describe the modelling techniques used to forecast ant invasions and summarize their predictions and (III) point to necessary developments of invasion forecasts under climate change.

### Pathways and mechanisms

The invasion pathway can be described as a series of distinct stages, and the transition between any two stages is hindered by specific barriers (HELLMANN & al. 2008, BLACKBURN & al. 2011) (Fig. 3). First, a native species needs to be transported, overcoming geographic barriers. Second, the individuals introduced outside their native range need to survive under the environmental conditions of the recipient area. Next, the population needs to be able to reproduce and achieve a positive growth rate in order to truly establish itself in the new environment, which means overcoming interspecific interactions and being able to spread across the landscape. Although still subject to debate, the generation of impacts can constitute the last stage of invasion. Obviously, biotic and abiotic barriers are not as distinct as pictured in Figure 3, but abiotic factors and, in particular, climatic suitability, are considered a prerequisite for a species to be introduced into a novel area. All stages of the invasion process might be affected by climate change in different ways (HELLMANN & al. 2008).

**Transport:** 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 among countries (ESSL & al. 2011). Some are simply introduced by accident with cargo (MACK & al. 2000). The recent increase in human commerce and tourism has transported more than 200 ant species all over the world (SUAREZ & al. 2010). Previously, ants had been unable to colonize many mid-Atlantic and Pacific islands (but see MORRISON 2014). For example, Hawaii has no native ant fauna, but today there are approximately 50 ant species, introduced mostly during the 20<sup>th</sup> century (KRUSHEL-

NYCKY & REIMER 2005). To better understand the patterns of spread of invasive ants, researchers have retraced 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 (SUAREZ & TSUTSUI 2008, FOUCAUD & al. 2010, VOGEL & al. 2010, VAN WILGENBURG & al. 2010, ASCUNCE & al. 2011). Overall, these studies demonstrate that introductions occur at a large scale, mainly linked to long-distance dispersal by humans. Therefore, it is essential to understand on which types of commodities invasive ants usually arrive. The vast majority (> 90%) of ant species introduced to the US occur on diverse plant material, mostly on orchids and bromeliads and some on fruits, other ornamental plants and Acacia trees (SUAREZ & al. 2005). 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 (MCGLYNN 1999b, MIRAVETE & al. 2014). However, 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 (SUAREZ & al. 2009 and references therein). Climate change could alter patterns of tourism, transport and commercial exchanges, potentially modifying propagule pressure (HELLMANN & al. 2008). For example, new routes are likely to be open due to ice openings in northern seas. Additionally, climate change may improve the survival probability of many ornamental plants in regions that are now unsuitable for them, and an increase in trade of plants in new regions may be associated with an increase in ant introductions, both in terms of propagule pressure and species number. In addition, climate change might alter the probability of ant colonies surviving during transport (HELLMANN & al. 2008), both because climate will be milder for many journeys and because transport will be shorter thanks to new route openings.

**Survival:** An exotic species has to be introduced to a region with favourable abiotic conditions in order to survive (Fig. 3). Climatic conditions, in particular, can influence the survival of invasive species at a local scale (JAMES & al. 2002, XU & al. 2009). Inter-annual variation in rainfall is a good predictor of regional dynamics of the invasion front, determining local survival rates of *Linepithema humile* colonies (HELLER & al. 2008, GORDON & HELLER 2014) and, ultimately, the rate of invasion (HOLWAY 1998). Experimental *L. humile* nests under different temperatures in the lab will collapse if the soil temperature is below 5 °C for more than eight days because the ants cease foraging at this temperature and end up starving to death (BRIGHTWELL & al. 2010). This estimation coincides with the observed patterns of *L. humile* invasion in the United States and is thought to be limited by winter soil temperatures (BRIGHTWELL & al. 2010), which is likely to be a limiting factor for many other invasive ants. Notably, compared with six ant species native to the United States, the Argentine ant ranked lowest in their ability to tolerate heat stress and to forage under high temperatures (HOLWAY & al. 2002). Similarly, *Brachyponera chinensis*, an invasive ant that is spreading throughout the United States, has a low thermal tolerance (39 °C) compared to the median critical thermal maximum of ants (43.3 °C) (DIAMOND & al. 2012). Because climate change will affect all climatic vari-

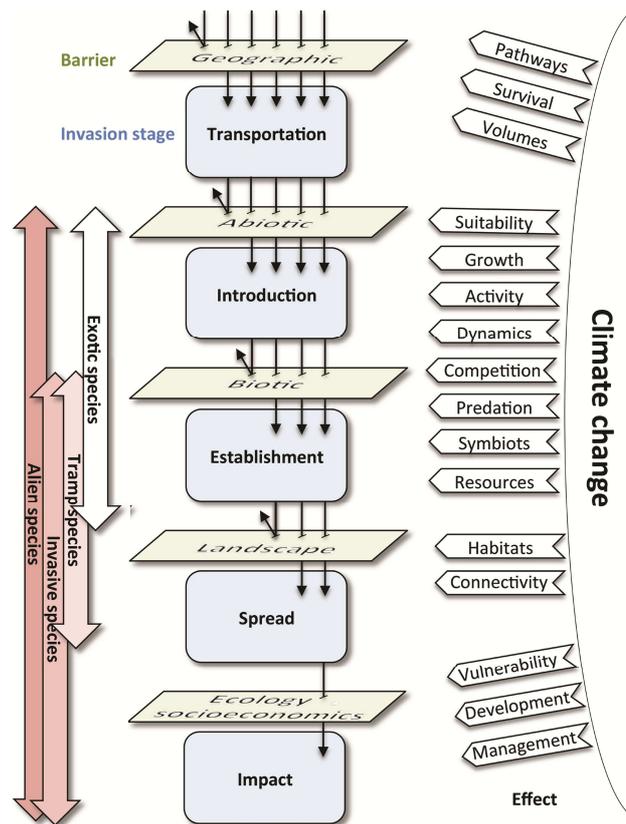


Fig. 3: Conceptual model of the process of ant invasions, outlining five stages of invasions (blue boxes), separated by five types of barriers (named after their main characteristics; green sheets) and the nature of the potential effects of climate change (white arrows, pointing towards a general stage level). The range of stages at which a given ant species is found defines its denomination (red, vertical arrows). Modified from HELLMANN & al. (2008).

ables, it will modify the probability of survival in a given place.

**Reproduction:** Many features of ant reproductive biology are temperature-dependent. For example, oviposition rates of Argentine ants are optimal at 28 °C and completely cease below a given temperature threshold (ABRIL & al. 2008). In addition, different developmental stages (eggs, larvae, pupae, adult production) have different minimum and maximum temperature thresholds for this species (ABRIL & al. 2010). This is an important factor for determining invasion success, because the colony has to complete at least one colony cycle to establish itself.

Recently, it has been shown that the range of thermic tolerances of individual workers can lead to an overestimation of the range of tolerances of colony growth (DIAMOND & al. 2013). More studies on the effect of climatic variables on colony dynamics should be performed in order to obtain a good understanding of the response curve of colony growth depending on temperature (e.g., PORTER 1988).

**Spread:** Climate changes could create opportunities for ant species to spread and invade new habitats, particularly at higher latitudes. 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 (THOMAS & HOLWAY 2005, SCHILMAN & al. 2007). However, even without a great degree of heterogeneity of the habitat, climatic variables can influence the rate of spread. For example, rainfall has been shown to facilitate the spread of *Linepithema humile*, suggesting that increasing rainfall will promote a wider distribution of Argentine ants and increase their spread into new areas in California (HELLER & al. 2008). However, regional climate models suggest that both winter and summer precipitation will decrease in California (HELLER & al. 2008), suggesting that the species could not benefit from climate change in these areas.

Even when a population has been able to successfully establish itself and reproduce, it might not be able to spread. The propagation in a heterogeneous landscape can depend on environmental barriers in addition to population dynamics (growth rate, generation of dispersing propagules). This is the case if the population has been introduced in a greenhouse or buildings situated in a globally unfavourable environment. Similarly, urbanization has led to urban heat islands as much as 12 °C hotter than their surroundings (ANGILLETTA & al. 2007), offering opportunities for exotic ants adapted to a warmer climate. Under the ongoing climate warming, urban areas can therefore act as refuges until the microclimatic conditions of surrounding areas become favourable to species spread.

**Impact:** The impacts of invasive ants also depend on the environmental conditions, yet very few researchers have investigated the effect of climate change on the impacts of invasive species. Climate change may benefit invasive species by increasing climatic suitability for them and by weakening the biotic resistance of the native communities. Already, predictions suggest that climate change will threaten many species in general (BELLARD & al. 2012) and many native ants in particular (FITZPATRICK & al. 2011, PELINI & al. 2014), and climate change may have detrimental effects on invasive ant species. Ant communities are predicted to be affected, especially in warm and rich regions (FITZPATRICK & al. 2011, DIAMOND & al. 2012, DIAMOND & al. 2013, PELINI & al. 2014). Even within communities, species are differently affected by warming. Xeric and tropical habitats are, for example, characterized by dramatic spatial heterogeneity in temperatures, particularly in the transition from sun to shade (KASPARI & al. 2015). This patchiness generates differences in the thermal adaptation of ant species. Body size may also determine species' thermal tolerance: Large ants remain active at higher surface temperatures than small ants (KASPARI & al. 2015). Some native species will suffer from climate change because it will push them beyond their climatic niches or because some key species in their community will be affected.

Climate change is predicted to affect native species quite heterogeneously (PELINI & al. 2012, STUBLE & al. 2013, PELINI & al. 2014), so even if they remain able to persist under the changing environmental conditions, it is possible that they will survive under sub-optimal conditions, rendering them weaker in interference or resource competition (e.g., because they experience too few days and hours within their range of optimal foraging temperatures). If the novel environmental conditions correspond to the optimal climatic niche of the invader, the species will have an advantage over the native persisting species, ren-

dering the competitive displacement of other species more likely. The contrary is also possible. Invasive ants often have a weaker tolerance to heat compared to the native species in their invaded range and forage at lower temperatures (HOLWAY & al. 2002). It is possible that the daily foraging periods of the invader will be even shorter, conferring an advantage on the native community, if it manages to persist.

### Forecasting ant invasion

**Species distribution models:** Species distribution models (SDMs) have become increasingly widespread as a tool to forecast the future of biodiversity (BELLARD & al. 2012), and they have been applied in several studies to predict invasive ant distributions (see, for example, the references in Tab. 1). One of the greatest advantages of this method is that it requires only species occurrence data as input, and it 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 are mapped, and each occurrence point is matched with a set of climatic variables (e.g., mean annual temperature, rainfall of the wettest month). Then, an algorithm is applied to describe the relationship between a species' current distribution and the climatic data. This relationship (model) can be subsequently projected onto maps of current or future climates to identify areas of suitable climatic conditions.

However, predictive maps should be viewed as mapping the range of habitat that presents a certain number of the species' abiotic requirements rather than a concrete forecast of species invasions. Indeed, SDMs include implicit assumptions and methodological limitations that constrain their predictive power. Range predictions vary with the variables considered to model a species' niche (FITZPATRICK & al. 2007), with the environmental data sets (PETERSON & NAKAZAWA 2008), with the quality of the species distribution dataset, with the spatial and temporal scales (HULME 2003) and with the correlative statistical methods (HARTLEY & al. 2006, ROURA-PASCUAL & al. 2009b). Furthermore, correlative niche models do not take into account biotic interactions, dispersal capacities and phenotypic plasticity or evolutionary adaptation and niche shifts (BROENNIMANN & al. 2007, FITZPATRICK & al. 2007, ROURA-PASCUAL & SUAREZ 2008, STEINER & al. 2008, GALLAGHER & al. 2010), all of which are decisive for ant invasion success or failure. Empirical comparisons with ant species distributions have shown that some widely used SDM models, such as Maxent, have significant limitations (FITZPATRICK & al. 2013).

Despite these limitations, niche models still provide an important and useful tool as a coarse assessment of whether an ant species is likely to invade a given region. A certain number of studies have used these correlative species distribution models to explore the current potential range of invasive ant species and the appropriateness of different modelling methods (e.g., HARTLEY & al. 2006, FITZPATRICK & al. 2007, WARD 2007, PETERSON & NAKAZAWA 2008, STEINER & al. 2008). However, these forecasts predict invasions under current climatic conditions; future invasions will take place under different climatic conditions. Therefore, it is surprising that few studies have

Tab. 1: Table of origin, impact examples, and climatically suitable regions (currently and with climate change) for the 19 invasive ants species. Unreached suitable regions (\*) are all based on species distribution models in BERTELSMEIER & al. (2015), for all species, as well as in ROURA-PASCUAL & al. (2011) and HARTLEY & al. (2006) for *Linepithema humile*; in WARD (2007) for *Paratrechina longicornis* and *Technomyrmex albipes*, and in MORRISON & al. (2005) for *Solenopsis invicta*. Likely impact of climate change (\*\*) based on BERTELSMEIER & al. (2015), for all species, and on (a) CHEN (2008), (b) ROURA-PASCUAL & al. (2004), (c) COOLING & al. (2012), (d) BERTELSMEIER & al. (2013a), and (e) MORRISON & al. (2005). Climatic suitability studies are not available for three species (noted with a "?"). Key references for the impacts are given in RABITSCH (2011) and in LACH & HOOPER-BUI (2009).

Scientific name	Common name	Region of origin	Examples of impact	Unreached suitable regions*	Likely impact**
<i>Acromyrmex octospinosus</i>	leaf-cutting ant	South America	defoliates trees and plants, mainly fruit crops and monoculture plots of mahogany as well as tree ferns in primary forests	Unknown suitable regions	?
<i>Anoplolepis gracilipes</i>	Yellow crazy ant	Asia or Africa	displacement of endemic species, disruption of ecosystem processes, agricultural damages, spraying of irritating formic acid	Central and South America, West Africa, Madagascar, USA, New Zealand	-   + a
<i>Linepithema humile</i>	Argentine ant	South America	displacement of native ants and other arthropods, disruption of ecosystem processes (pollination, seed dispersal)	Central Africa, Madagascar, China, Eastern Europe, Great Britain, Scandinavia	--   -   + b   c
<i>Lasius neglectus</i>	Invasive garden ant	Asia Minor	displacement of native ants, negative impacts on invertebrate communities, house infestation, damage to electric devices	USA, Canada, China, Japan	=
<i>Monomorium destructor</i>	Destroyer ant	India	damage to electric devices and property, painful sting, transmission of diseases	No entirely new regions	++
<i>Monomorium floricola</i>	Flower ant	Asia	negative impacts on native ants, butterflies, coconuts, silkworms	Madagascar	=
<i>Monomorium pharaonis</i>	Pharao ant	Africa	house infestation, disease transmissions	New Zealand, Mediterranean	+
<i>Myrmica rubra</i>	European fire ant	Europe, Central Asia	displacement of native ants, negative impacts on invertebrate communities, nuisance to humans and pets, painful sting	South America, Southeast Asia, Australia, New Zealand, East of North America	=
<i>Nylanderia pubens</i>	Caribbean crazy ant	Caribbean	nuisance to humans, pets and livestock, dessication of grassland, electrical equipment damage, likely effect on biodiversity	Unknown suitable regions	?
<i>Pachycondyla chinensis</i>	Asian needle ant	East Asia	displacement of native ants, disruption of an ant-plant seed dispersal mutualism	Unknown suitable regions	++ d
<i>Paratrechina longicornis</i>	Crazy ant	Asia or Africa	displacement of native ants, negative impacts on invertebrate communities, house infestation, disease transmissions	New Zealand	+
<i>Pheidole megacephala</i>	Big-headed ant	Africa	displacement of native ants, negative impacts on invertebrates and vertebrates, agricultural damages, damages to electric devices	India, Egypt, New Zealand, East of North America	--
<i>Solenopsis geminata</i>	Tropical fire ant	Central America	negative impacts on animal and plant communities, damages to electric devices, painful sting, house infestation, damages to agriculture, disease transmissions	New Zealand	++
<i>Solenopsis invicta</i>	Red imported fire ant	South America	negative impacts on many native plants, invertebrates and vertebrates, painful sting (anaphylaxis may lead to death), high economic damage, damages to agriculture	Carribeans, Africa, Madagascar, Southeast Asia, India, Japan, Australia, Indonesia, Mediterranean	++   + e
<i>Solenopsis papuana</i>	Papuan thief ant	South Pacific	displacement of native invertebrates, in particular spiders	Unknown suitable regions	?
<i>Solenopsis richteri</i>	Black imported fire ant	South America	painful sting (anaphylaxis may lead to death)	Europe, Australia, New Zealand	-
<i>Technomyrmex albipes</i>	White-footed ant	Indo-Pacific	house infestation, disease transmissions	North, Central and South America, Carribeans, Central and North Africa, Middle East, New Zealand	--
<i>Tapinoma melanocephalum</i>	Ghost ant	Asia or Africa	house infestation, disease transmissions, skin irritation	New Zealand	=
<i>Wasmannia auropunctata</i>	Electric ant	South America	displacement of native invertebrates and vertebrates, damages to agriculture, painful sting (anaphylaxis), disease transmissions	Europe, Madagascar, India, Southeast Asia, New Zealand	--

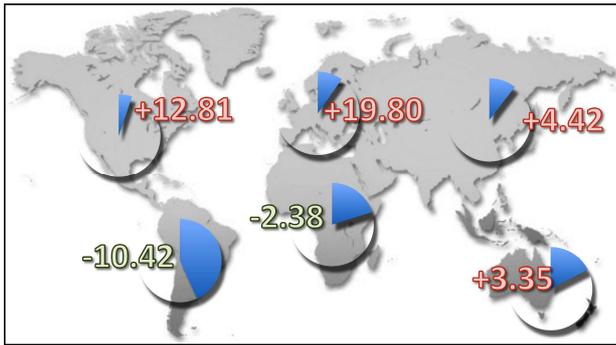


Fig. 4: Average predicted proportion of climatically suitable landmass on each continent for 15 invasive ants (see Tab. 1) studied in BERTELSMEIER & al. (2015) (blue pie chart) and predicted change following climate change (red percentage indicates an increase in range, green percentage indicates a decrease).

considered these future climatic conditions in their predictions (see references in Tab. 1). This is especially so because climate change is widely recognized as a major factor determining species' distributions in the future (ROURA-PASCUAL & SUAREZ 2008, ROURA-PASCUAL & al., 2011).

SDM studies that have explicitly included the effect of climate change on projected range sizes have predicted a positive effect of climate change on the global distribution of the yellow crazy ant, *Anoplolepis gracilipes* (see CHEN 2008); the destroyer ant, *Monomorium destructor* (see BERTELSMEIER & al. 2015); the pharaoh ant, *Monomorium pharaonis* (see BERTELSMEIER & al. 2015); the long horn crazy ant, *Paratrechina longicornis* (see BERTELSMEIER & al. 2015); the tropical fire ant, *Solenopsis geminata* (see BERTELSMEIER & al. 2015); the red imported fire ant, *Solenopsis invicta* (see MORRISON & al. 2005, BERTELSMEIER & al. 2015); and the Asian needle ant, *Brachyponera chinensis* (see BERTELSMEIER & al. 2013a) (Tab. 1). *Brachyponera chinensis* is a fairly new invader and has been added to the ISSG database only recently (IUCN SSC INVASIVE SPECIES SPECIALIST GROUP 2012). Its population has shown especially large increases in Europe, Oceania and North America (BERTELSMEIER & al. 2013a). It is possible that some of the invasive species benefitting most from climate change will not be part of the "usual suspects" of currently highly invasive ants but may be some emergent invaders that have not yet had the opportunity to invade under current climatic conditions.

Invasive ants can benefit from climate change not only by increasing their total suitable range but also by increasing the relative suitability within their potential range (or "habitat quality"). A case study with two invasive ants estimated the 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 (BERTELSMEIER & al. 2013b). Both ant species were predicted to benefit from climate change, but in different ways. The size of the potential distribution increased by 35.8% for *M. destructor*. Meanwhile, the total area of potential distribution remained the same for *M. rubra* (> 0.05%), but the level of climatic suitability within this range increased greatly and led to an improvement in

habitat quality and, thus, of its likelihood of establishment (BERTELSMEIER & al. 2013b).

However, not all invasive ants will benefit from climate change (Tab. 1). At a global scale, *Linepithema humile* has been projected to decrease in potential range (-11 to -15%, according to the climate change scenario), retracting in tropical regions but expanding at the same time at higher-latitude areas by 2050 (ROURA-PASCUAL & al. 2004). This contrasts with the projections by COOLING & al. (2012), who predicted an increase at a local scale (New Zealand). Similarly, *Anoplolepis gracilipes* has been projected to decrease at a global scale (BERTELSMEIER & al. 2015), contrary to the projections made by CHEN (2008). Another highly invasive species, the big-headed ant, *Pheidole megacephala*, has been predicted to decrease in range size and suitability on all continents and across all time horizons considered (2020 - 2080). The loss in suitable areas by 2080 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%) (BERTELSMEIER & al. 2013c). Four further species are predicted to suffer from climate change: the black imported fire ant, *Solenopsis richteri*; the ghost ant, *Tapinoma melanocephalum*; the white-footed ant, *Technomyrmex albipes*; and the electric ant, *Wasmannia auropunctata* (see BERTELSMEIER & al. 2015). Finally, three species are predicted to remain stable: the invasive garden ant, *Lasius neglectus*; the flower ant, *Monomorium floricola*; and the European fire ant, *Myrmica rubra* (see BERTELSMEIER & al. 2015).

The reason some invasive ant species are predicted to increase with climate change while some others should decrease might be due in part to the methodological disparities. Overall, the predictions of different studies are not easily comparable because they use a variety of different model inputs. They vary in the number of climatic variable types considered, the spatial extent of the study, the spatial resolution, CO<sub>2</sub> scenarios, Global Circulation Models (GCMs) and the modelling methods used. However, a recent study has used a single methodological framework to project the impact of climate change on 15 invasive ant species and found that there was no homogeneous trend across species and regions (BERTELSMEIER & al. 2015). There was a considerable heterogeneity in responses to climate change across all continents (Fig. 4), 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 (MITTERMEIER & al. 2012). Following climate change, the models predicted that the proportion of suitable areas within the biodiversity hotspots would increase even further for five species: *Monomorium destructor* (+ 19.7%), *Solenopsis invicta* (+ 16.3%), *Paratrechina longicornis* (+ 8.5%), *Solenopsis geminata* (+ 7.4%), and *Monomorium pharaonis* (+ 3.7%) (BERTELSMEIER & al. 2015). The disparities in the effect of climate change, both globally and in the hotspots, are apparent despite a common methodological framework and should therefore rather reflect differences in the species ecophysiology.

Overall, invasive ants are likely to remain an important threat, and it is important to prioritize areas and species

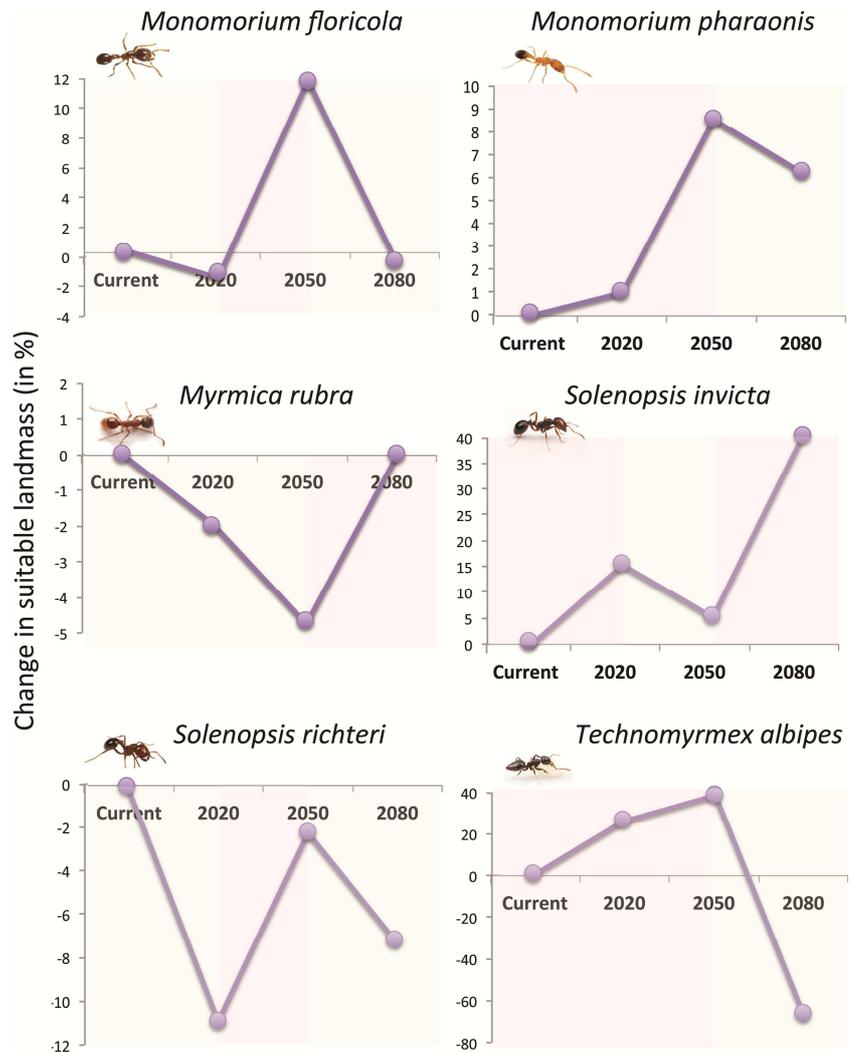


Fig. 5: Quantitative changes in potential habitat relative to the species' current potential habitat for three dates in the future (2020, 2050, 2080) for the six species. Zones in green show a decrease in suitable habitat, zones in red show an increase. Scale is kept different among species to focus on trend reversal, as comparison between species is not relevant here. After BERTELSMEIER & al. (2013d). The ant icons are modified versions of Alex Wild's photographs.

for surveillance efforts. One study chose 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 they present for different species under current and future climatic conditions (BERTELSMEIER & COURCHAMP 2014). This follows current calls by the scientific community to apply species distribution models for concrete recommendations (DAWSON & al. 2011, GILLSON & al. 2012, SUMMERS & al. 2012, KUJALA & al. 2013).

However, conservation actions taking climate change projections into account can be based on different time horizons in the future. A study using the same 15 invasive ant species has tested the influence of the choice of the time horizon on projections by forecasting potential distributions in 2020, 2050 and 2080 (BERTELSMEIER & al. 2013d). Surprisingly, 6 of 15 species showed "trend reversals", i.e., an initial increase of suitable areas followed by a decrease, or vice versa (Fig. 5). These trend reversals are unlikely to be due to "noise" in the projections, to certain future climatic scenarios or to the choice of a particular classification threshold. A possible explanation 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 total area

that corresponds to the climatic conditions under which the species can thrive may also be present in a smaller amount of landmass. Further, it is possible that the suitable area increases and shifts in space at the same time, reaching a geographic barrier (e.g., the ocean). When the suitable area continues to shift in that direction, this leads to a net decrease in suitable landmass and, therefore, a "trend reversal". These findings illustrate the importance of making forecasts for several time horizons in the future to identify this type of pattern, a strong conservation message that goes well beyond invasive ant species.

A general hypothesis made by all SDMs is that the species is in equilibrium with its environment (i.e., that the current distribution reflects its ideal climatic conditions). However, when trying to predict invasions under climate change, one makes a double extrapolation, in time and in space. For many invasive species, models can still serve as a good approximation (PETITPIERRE & al. 2012), but there are examples where the current distribution might not entirely reflect the species' potential to invade new areas. For example, the invasive populations might adapt to new environmental conditions (i.e., display a "niche shift"). The ability of *Wasmannia auropunctata* to withstand the harsh conditions may have been selected at the range margins of its native distribution, before the introduction to a new

habitat, enabling the species to survive under colder temperatures and less rainfall (REY & al. 2012). 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 the upper and lower lethal temperatures of *Linepithema humile* workers to vary by several degrees after a period of four different acclimation temperatures (JUMBAM & al. 2008).

SDMs can also be used to test the niche equivalency of native and invasive populations or to compare different invasion scenarios. This has been done using reciprocal projections (i.e., a model calibrated on the native distribution and projected on the invaded range and vice versa), suggesting that the red-imported fire ant, *Solenopsis invicta*, from a peripheral native population, probably established itself in environments similar to its native range, but it subsequently invaded harsher environments (FITZPATRICK & al. 2007). On the other hand, *Linepithema humile* has been shown to display general niche conservatism, despite different geographic and community contexts (ROURAPASCUAL & al. 2014).

If the objective of a study is the prediction of a future range, it is currently best practice to include occurrence points from both native and invaded regions in order to include the full set of environmental conditions under which the species can thrive (BEAUMONT & al. 2009, RÖDDER & LÖTTERS 2009, LIU & al. 2011), but this method does not preclude the possibility that the species' niche might evolve in the future.

**Mechanistic models:** Unlike correlative SDMs, mechanistic models use the realized niche, i.e., the part of the fundamental niche that an organism occupies as a result of limiting factors or biotic interactions in its habitat, to make inferences about the optimal climatic conditions for the species. Mechanistic models derive the response curves directly from physiological data (i.e., the fundamental niche) to make projections. 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 & LESTER (2003) developed a model for *Linepithema humile* 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. This model 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. The model has been tested at an independent site, in Haleakala National Park (Hawaii) and has been shown to predict well the suitable sites for *L. humile* invasion over a period of 30 years (KRUSHELNYCKY & al. 2005). However, it has been argued that this degree-day model overestimates the potential range of that species and that another mechanistic model, based on brood survival and oviposition rates at different temperatures, yields more precise predictions (ABRIL & al. 2009).

Another mechanistic model used minimum and maximum daily temperatures to predict the production of sexuals in *Solenopsis invicta* (see MORRISON & al. 2004), based on an earlier study that had estimated a minimum number

of 3900 alates needed to ensure a given colony reproduction success (KORZUKHIN & al. 2001). A minimal precipitation condition was added to the temperature-based projection by superposing a map with sufficient rainfall for colony survival (MORRISON & al. 2004). 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 in the eastern United States of 4% by 2050 and of more than 21% by the end of the century (MORRISON & al. 2005). Another study used the mechanistic CLIMEX model to link colony growth and stress responses in *S. invicta* to temperature and moisture, and it identified areas along the west coast of the United States that might be invaded in the future (SUTHERST & MAYWALD 2005).

Although mechanistic models are useful to identify the relevance of fine-scale heterogeneity, it remains an important challenge to scale-up to link the relevant variables to broad-scale climate. In this context, a study has used past records of the progression of the invasion front in Haleakala National Park, which was linked to microclimatic data and population dynamics (HARTLEY & al. 2010). The rate of population expansion showed a linear relationship with the number of degree-days.

The main limitation of mechanistic models is that they need a large amount 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 (ABRIL & al. 2008), foraging at different temperatures (HELLER & GORDON 2006) and upper lethal thermal limits (JUMBAM & al. 2008), different predictions are obtained. In addition, the relevant limiting factor that determines the distribution of the species may be missed. Because of the higher data requirements for mechanistic models, it is very difficult to envision a comparative approach that assesses the relative invasion risk of many ant species, which are particularly interesting in non-equilibrium situations (e.g., climate change, invasions) (KEARNEY & PORTER 2009). However, these models have the potential to yield more accurate predictions.

Both SDMs and mechanistic models predict suitable areas for a given species. However, neither takes into account dispersal potential and limitations or the progression of the invasion.

**Spatially explicit spread models:** 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 two to five orders of magnitude greater than local dispersal in *Lasius neglectus* (see ESPADALER & al. 2007). Accordingly, global spread models can comprise two different linked models, one simulating local dispersal and the other long-distance transport to estimate the rate of invasion and to pinpoint areas at particular risk (SCANLAN & VANDERWOUDE 2006, PITT & al. 2009, SCHMIDT & al. 2010). The spread model can be calibrated with the observed historic spread of the species.

Dynamics at the invasion front have been simulated using reaction-diffusion models (SHRYOCK & al. 2008). It has been suggested that known dose-response establish-

ment curves that estimate the propagule pressure needed for the species to colonize a new area should be incorporated in spread models (MIKHEYEV & al. 2008).

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 *Solenopsis invicta* around Brisbane, Australia, it was calculated that more than twice as many fire ant nests could have been found using this spread model compared to random searches. This might significantly improve the chances of eradicating the species (SCHMIDT & al. 2010).

Spread models can be a complementary approach to SDMs or mechanistic models by, for example, identifying probable points of entry within at-risk suitable areas that can be identified by a niche model. Ideally, both types of approaches can be linked (ROURA-PASCUAL & al. 2009a). The SDM or mechanistic models provide a suitability map for a focal species, and the coupled spread model simulates the progression of the invasion within the suitable landscape at a local scale. Recently, several studies have combined habitat suitability (or climatic suitability) with a spread model. For instance, the spread of *Linepithema humile* has been modelled with a grid-based invasion model, similar to a cellular automaton, combined with habitat and climate variables in order to forecast the species' invasion in the Jasper Ridge Biological Reserve (California) over the next few decades (FITZGERALD & al. 2012). These models can be used to test hypotheses about the invasion dynamics within a suitable area. Using historical data of *L. humile* spread in New Zealand, PITT & al. (2012) have shown that a uniform spread model was effective at predicting populations early in the invasion process, but later on, a spatially explicit stochastic model was more accurate. Although the coupling of SDM / mechanistic models with spread models can yield a more precise prediction at a local scale, it has not yet been applied to forecasts involving the impacts of climate change on future ant invasions.

### Developments of invasion forecasts

Current forecasts of ant invasions under future climate change can serve as an interesting baseline, but they suffer from a range of limitations. In particular, biotic interactions can ultimately modify the distribution of invasive ants, and the community context can greatly influence the species response to climate change. In addition, behavioural mechanisms such as nest site selection and phenological plasticity can buffer against the impacts of climate change. Further global changes can, in some cases, also lead to synergistic effects on ant invasions. In this section, we will discuss evidence for the impacts of these potential "moderating" factors that can lead to a deviation of the response from the projections based on classical SDMs. We will focus on methodological improvements of existing methods and briefly introduce a new generation of integrative hybrid models.

**Biotic interactions:** Biotic interactions are very important factors that should be taken into account, as they can change under climate change. For example, interactions with other invasive ant species can be a factor hindering invasion success. Behavioural assays have shown that *Anoplolepis gracilipes* attacks, kills and repels foraging *Solenopsis invicta* workers at baits where they co-occur (ZHENG

& al. 2008). 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, *Linepithema humile* and *S. invicta*, display an invasive syndrome in their native range. Here, strong interspecific competition is likely to be an important limiting factor (LEBRUN & al. 2007). It is important to test interspecific competition among the worst invasive ant species to couple the future range predictions of these species with the effect of competition at a local scale. Recently, an experimental approach has been used to establish a dominance hierarchy among seven of the worst invasive ant species that could co-occur following climate change (BERTELSMEIER & al. 2015). Importantly, it remains to be investigated how relative competitive abilities are modulated by environmental variables (RICE & SILVERMAN 2013, BARBIERI & al. 2015) to incorporate them in future forecasts.

A community model has been developed recently to predict future coexistence in a well-studied native North American ant community, parameterized using thermal niches, food discovery rates and historical species co-existence (BEWICK & al. 2014). This model was then used to predict how the community will restructure in response to climate-related changes such as increased temperature, shifts in species phenology, and altered resource availability. Interestingly, the most heat-sensitive species were not those most at risk of extinction (BEWICK & al. 2014). Some species traits (e.g., leg length) have been linked to responses to climate change and changes in community composition at a local scale in ant communities in Florida (WIESCHER & al. 2012). A different approach to multi-species predictions has been developed using generalized dissimilarity models (GDMs), which model compositional dissimilarity, i.e., spatial turnover of species composition, between all pairs of locations within the study area as a function of environmental differences between those locations (FITZPATRICK & al. 2011). This spatial relationship between species composition and environmental variables can be transposed in time in order to predict future community compositions under climate change (FITZPATRICK & al. 2011). For community predictions, it can be very useful to calibrate the models based on past, observed changes in ant community composition and relate them to changes in climatic variables (RESASCO & al. 2014). The incorporation of the projections for focal invasive species with predictions for impacts of climate change on the recipient ant communities would be a great qualitative advance in this field. Such an integration, however, is not straightforward because biotic and abiotic factors limiting the distribution of invasive species are scale-dependent processes interacting in complex ways (MENKE & al. 2007).

In addition to competitive interaction with other ants, it would be interesting to investigate how mutualisms will respond to climate change. Facilitation, such as through the association with honeydew-producing insects, is another important biotic interaction during invasions (LACH 2005, GROVER & al. 2007, HELMS & VINSON 2008, OLIVER & al. 2008, ROWLES & SILVERMAN 2009, SAVAGE & al. 2011, WILDER & al. 2011, SHIK & SILVERMAN 2013). The availability of carbohydrate sources can favour ant abundance and spread (ROWLES & SILVERMAN 2009) as well as colony size (HELMS & VINSON 2008, WILDER & al. 2011). It

can also increase patrolling behaviour in worker ants and lead to lower colony mortality and higher final colony sizes (KAY & al. 2010). 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 (GROVER & al. 2007). It has been estimated that honeydew produced by Homoptera in Texas supplies half the daily energetic requirements of a *Solenopsis invicta* colony and that 70% of that comes from only one species of invasive mealybug, *Antonina graminis* (see HELMS & VINSON 2002). Fire ants in the United States occupy a significantly lower trophic position compared with those in the native range, and *S. invicta* shifts from protein resources (insects prey) in its native range to mutualist-provided carbohydrates in its introduced range (WILDER & al. 2011). Argentine ants depend strongly on carbohydrates in the centre of the invaded range, while relying on a more protein-enriched diet at the invasion front (TILLBERG & al. 2007). An experimental temperature manipulation showed that warming reduced the abundance of aphids because the local tending ant species, the winter ant *Prenolepis imparis*, was less aggressive towards predators (BARTON & IVES 2014). In the same way, invasive ants might be affected by the indirect impacts of climate change on the mutualism with honeydew-producing aphids, which have been shown to be sensitive to climate change (BELL & al. 2015).

**Behavioural mechanisms:** Ant behaviour is, to some degree, flexible, and it adjusts under changing environmental conditions. It can thus buffer against the effects of climate change, through either temporal or spatial flexibility. Invasive ants may not experience the same climatic conditions as native ants (which themselves experience a variety of microclimatic conditions), even in the same habitat. In some cases, native and exotic ants have different temporal niches and switch dominance according to seasons (CERDÁ & al. 2013). On Okinawa Island, Japan, seasonal activity patterns were different between exotic and native ants, the native species being dominant only in spring and summer (SUWABE & al. 2009). On a daily basis, the dominance of invasive ants can change with temperature as well (CERDÁ & al. 2013). In Western Australia, *Linepithema humile* can only displace native ants from food baits in the morning (THOMAS & HOLWAY 2005). In addition, the impacts of climate change on the foraging rates of ant species can depend on body size, changing inter-specific resource competition (SEGEV & al. 2014). Within the same ant community, different ant species modify their foraging rates in different ways to elevated temperature, with some species foraging more under higher temperatures and others less (STUBLE & al. 2013). The behavioural plasticity of habitat use is, therefore, a critical aspect of species' sensitivity to climate warming and extreme events (SUNDAY & al. 2014). These relative changes will be important in determining the impacts of climate change; classical SDM or mechanistic models do not account for these behavioural changes of multiple species within the same generally suitable climatic conditions. Similarly, classical SDMs do not account for adaptive differentiation among populations in response to different climatic conditions, and complementary methods have to be used to explore differences among populations (REY & al. 2012).

Alternatively, or concomitantly, ants may respond to climate change through behavioural mechanisms that involve spatial flexibility. It is important to investigate how invasive ants behave in a heterogeneous environment and how they adjust their nesting location to differences in microclimatic conditions. Ants are known for thermoregulation in their nests by selecting their nest sites and optimizing their nest structures to permit passive heating or cooling. They are also known for behaviours such as brood translocations to regions within a nest where temperatures are the most favourable (JONES & OLDROYD 2007). The soil temperature experienced by the ants can be very different from the surface temperature (KRUSHELNYCKY & al. 2005). In deserts, for example, ants nest in the cooler soil belowground and survive even though the surrounding temperature exceeds their lethal temperature. Moreover, many invasive ants are noted for their ability to relocate their nests and alter foraging networks in a flexible way in order to adjust temperature and humidity conditions (HELLER & GORDON 2006). This temporal and spatial fluidity in colony structure is thought to constitute one of the keys of the invasion success in many ant species (SUAREZ & TSUTSUI 2008). In addition, when assessing the invasiveness of a particular region, fine-scale variation in microclimatic conditions should be taken into account. Even when a large-scale SDM / mechanistic model predicts unfavourable climatic conditions, it is possible that invasive ants will find suitable microclimatic conditions by changing their nesting location. It remains to be investigated to what extent such behavioural flexibility can buffer against the effects of climate change.

**Phenological plasticity and evolutionary change:** It has been suggested that thermal variability plays an important selective role in life-history traits (FOLGUERA & al. 2011). For insects, increased ambient temperatures have direct consequences for metabolic rates and developmental rates (DILLON & al. 2010). In ants, temperature affects both the survival of individuals and different components of colony fitness, particularly reproduction (DIAMOND & al. 2013). For instance, temperature can affect both the queen's oviposition rate (ABRIL & al. 2008) and the development time from egg to adult worker (PORTER 1988, ABRIL & al. 2010). The lifetime reproductive success of ant colonies (i.e., the number of offspring colonies produced) may also be affected by temperature. Indeed, the production of sexuals (queens and males) is predicted to depend on colony size (TSCHINKEL 1993). Therefore, the faster a colony grows, the shorter the time to produce the first sexual ants should be. Temperature may also influence the queen's lifetime and thus indirectly alter the number of generations produced (INGRAM & al. 2013). From an ecological and evolutionary perspective, reproductive traits are important because additional brood per unit time may increase colony growth, decrease the time to produce sexual ants and accelerate adaptation. An earlier spring and a prolongation of the favourable period may therefore ultimately increase colony fitness.

However, the magnitude and the direction of the responses to warming are species specific, with some species expressing narrow phenotypic plasticity, leading to a decrease in their fitness, whereas other species are more plastic and able to cope with climate changes, increasing their long-term fitness (PELINI & al. 2012). Changes in en-

environmental conditions could therefore select for greater phenotypic plasticity. For instance, the ability of colony founding queens to tolerate a wide range of overwintering temperature may explain the success of the garden ant *Lasius neglectus* in urban areas (HAATANEN & al. 2015). Invasive species that are able to cope with new environments may take advantage of the ongoing climate change. To date, most research effort has been devoted to understanding the effects of temperature on foraging activity and the survival of workers. However, these proxies can affect the estimation of species distribution when calibrating models with the optimal temperature for the workers' survival rather than that for colony growth, which is lower (DIAMOND & al. 2013). As recently stressed by DIAMOND & al. (2013): "How warming impacts not only survival but also other components of fitness, particularly reproduction, is an important, but open, question in many systems." Future efforts should be devoted to build models that integrate different components of fitness, particularly reproduction.

**Interactions of climate change with other components of global change:** In addition to climate change, biodiversity will be exposed to other drivers of species extinction, in particular land use changes. Global studies projecting the future of biological invasions have started taking into account land use changes in parallel to climate change (BELLARD & al. 2013). However, forecasts of future ant invasions under climate change have not included projections of habitat modifications thus far, possibly because large-scale changes are less important for ants than for larger species (i.e., mammals or trees) because they establish themselves in micro-habitats. It has been shown that micro-climatic conditions are predictive of the thermal tolerance of ants (BAUDIER & al. in press). However, 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 the rate of spread of *Wasmannia auropunctata* into inner Gabon 60-fold (WALSH & al. 2004). Monitoring of the ant community immediately after clear-cutting forest in South Carolina revealed that *Solenopsis invicta* and *Pheidole* ssp. invaded the newly disturbed sites very rapidly (ZETTLER & al. 2004). Anthropogenic habitat modification, such as tree management in agroecoforests, can also promote the spread of invasive ants. For example, *Anoplolepis gracilipes* was frequently found in Indonesian cacao agroecoforests, and its presence was associated with decreased forest ant species richness (BOS & al. 2008).

Disturbance may also indirectly promote ant invasions. 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 (NAKAMARU & al. 2007). 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 (NAKAMARU & al. 2007). By selecting species that disperse by budding, disturbance indirectly favours invasive species because budding is the predominant mode of colony foundation. Moreover, human-modified habitats may have selected for male and female clonality in invasive populations of *Wasmannia auropunctata*, illustrating that humans not only disperse species but

also exert selective pressures over invasive species (FOUCAUD & al. 2010). Although disturbance frequently appears to be an important factor favouring ant invasions, some exceptions have been recorded (VANDERWOUDE & al. 2000, ROURA-PASCUAL & al. 2010). For example, *Solenopsis invicta* (see PLOWES & al. 2007, STUBLE & al. 2009), *Linepithema humile* (see HOLWAY 1995, SANDERS & al. 2001, KRUSHELNYCKY & al. 2005), *Anoplolepis gracilipes* (see O'DOWD & al. 2003), *P. megacephala* (see HOFFMANN & al. 1999, VANDERWOUDE & al. 2000), *Brachyponera chinensis* (see GUÉNARD & DUNN 2010) and *W. auropunctata* (see CLARK & al. 1982, WALKER 2006) have invaded many natural habitats.

Nevertheless, climate and human modification of habitats have been shown to be the most important determinants of the current distribution of *Linepithema humile* at a global scale (ROURA-PASCUAL & al. 2011), and the interaction between habitat modification and the presence of the invasive species can lead to the highest species loss (SALYER & al. 2014).

**New integrative tools:** A new generation of models is currently being developed that attempt to integrate competition, demography and dispersal in a heterogeneous landscape (KEITH & al. 2008). These so-called hybrid models, or niche-population models (NPMs), are a recent advance linking SDMs (or mechanistic range predictions) to a dispersal model and a population dynamics model (FORDHAM & al. 2013). As result, the dynamics of a metapopulation are simulated as a function of the suitability of local habitat patches, dispersal among colonized patches and the local population's growth and death rates (FORDHAM & al. 2013). In addition, in some cases, intra- and interspecific competition has been added to model the metapopulation dynamics. However, to calibrate and validate hybrid models, it is necessary to have spatial abundance data across the species' range (not just occurrence data, as in SDM models). These data are needed to establish the link between habitat suitability and population-specific parameters (for example, maximal growth rate, carrying capacity of the environment) (CABRAL & SCHURR 2010), which are rarely available. In addition to requiring more data, hybrid models are much more difficult to parameterise than simple SDMs, which potentially amplify uncertainty in model predictions (FORDHAM & al. 2013). In the future, it might be possible to build hybrid models for invasive ants, given the current research interest in many aspects of their biology. Ideally, a new generation of hybrid models should aim to integrate all steps of the invasion process framework (Fig. 3), starting with modelling the potential locations of introductions via commercial routes, and then link them to models of habitat suitability (SDMs), potential dispersal, population dynamics and metapopulations, with source-sink dynamics that can be modelled dynamically using a time series of future climate maps. However, even though hybrid models may be able to deliver more-accurate predictions at a local scale, they will not be easily applicable at a large scale or for a multi-species comparison (given the difficulties of model calibration), two points where SDMs provide interesting results.

## Conclusion

In this review, we have synthesized existing predictions of the future of ant invasions under climate change and have

attempted to separate the overall trends from the noise resulting from variable predictions. In particular, we have shown that invasive ants will not systematically benefit from climate change (BERTELSMEIER & al. 2013d); responses are predicted to be heterogeneous across ant species, spatial and temporal scales, evaluation metrics and modelling methods. Overall, despite an absence of a systematic increase in ant invasions following climate change, the number of invasive ants can increase locally, and several highly invasive ants will gain access to new regions.

The question remains whether it is possible to forecast ant invasions despite important model limitations. The variations among predictions partly stem from inherent uncertainties (e.g., choice of modelling method, future CO<sub>2</sub> emission scenarios) and partly from an incomplete understanding of biological processes (e.g., behavioural plasticity, species interactions). However, current models can still serve as an interesting "baseline" approximating global ant distributions and can be used to explore future scenarios. Nevertheless, as with any model, they should not be viewed as "accurate" predictions. To some extent, future models could improve predictions by attempting to incorporate more mechanistic variables, population dynamics, species interactions and dispersal data, but the predictions will always be limited by a certain amount of inherent model uncertainty. Future perspectives on the study of invasive ants under climate change include extending existing methods to qualitatively improve range prediction; accounting for the impacts of climate change on different stages of the invasion process that can indirectly influence the invasion risk; studying how species interactions and community composition will react to climate change; investigating behavioural mechanisms that can buffer against or amplify the impacts of changing environmental conditions; and accounting for changes in land use and the degree of disturbance. However, models will always face a classical trade-off between realism and generality. Some models will perfectly fit the local dynamics of an invasive population but will not be able to predict new invasions on a different continent.

Current approaches to predicting ant invasions already deliver useful approximations at a large spatial scale and might allow prioritizing species and areas for management actions. In the future, ant invasions are likely to remain a major problem, and it is possible that newly introduced invaders will benefit more from climate change than some of the species that are currently among the worst invaders. Therefore, it is not prudent to focus research efforts exclusively on today's "worst" invasive ant species.

### Acknowledgements

We thank Nùria Roura-Pascual for her comments on an earlier version of this paper. OB is funded by a Biodiversa Eranet grant, and FC is funded by a BNP grant and an ANR grant.

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