

The utility of species distribution models to predict the spread of invasive ants (Hymenoptera: Formicidae) and to anticipate changes in their ranges in the face of global climate change

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Abstract

Species distribution models that predict the geographic ranges of invasive species have received a lot of attention recently. This approach can be very useful for determining the potential for additional spread in invaded areas and for identifying new regions that may be susceptible to invasion. With the increasing availability of scenarios of future climate conditions, researchers also have a unique opportunity to anticipate changes in the geographic ranges of species that result as a consequence of global warming. However, it remains unclear to what extent distributional models can accurately estimate changes in the species' geography under climate change. This uncertainty results, in part, from some limitations inherent to distribution models. For example, they do not incorporate biotic interactions that can influence a species' distribution, and the abiotic conditions included in the model may not be the only ones necessary for accurately predicting an organism's geographic range. We review studies using both correlative and mechanistic models to assess the distribution of ant invasions to determine the state of knowledge on the topic, and also identify areas of future research required to understand the present-day and future consequences of global warming on the distribution of invasive ants.

Key words: Invasive ant species, species distribution models, correlative *versus* mechanistic approaches, climate change scenarios, review.

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Introduction

The Intergovernmental Panel on Climate Change (IPCC) recently presented its Fourth Assessment Report on the actions that different countries should follow to reduce the effects of man-made climate change, mainly caused by the emission of greenhouse gases on the atmosphere (SOLOMON & al. 2007). One of the main reasons for undertaking such protocols is to minimize the impacts of global warming on biodiversity (PENUÉLAS & FILELLA 2001, WARD & MASTERS 2007).

Climate change and land degradation are known to alter the distribution and abundance of species worldwide, by enhancing the loss of biological diversity and also the susceptibility of habitats to become invaded (TILMAN & al. 1994, MCCARTY 2001, WARREN & al. 2001). Biological invasions are not novel events, but the number of species that have been introduced into new ranges has increased exponentially over the last 200 years due to the increase in human mobility (CASTRI 1989). As a result, biotic invasions are not only a consequence but also a significant component of human-driven global change (VITOUSEK & al. 1996, SALA & al. 2000, HULME 2003). While the deliberate and accidental introduction of non-native species occurs

across many taxonomic groups (VITOUSEK & al. 1997), ants are particularly problematic with five species now recognized in the world's 100 worst invaders (MCGLYNN 1999, LOWE & al. 2000). They can have severe consequences on the economy and environment in the ecosystems they invade (WILLIAMS 1994, MACK & al. 2000, HOLWAY & al. 2002).

The consequences of climate change and biological invasions on biodiversity have received considerable attention (VITOUSEK & al. 1996, DUKES & MOONEY 1999, SALA & al. 2000). Many studies have focused on the effects of climate change on invasive species, and have used distribution models to estimate changes in their geographic ranges under different scenarios of global warming (reviewed in HEIKKINEN & al. 2006). Distribution modelling is an attractive tool for invasion biology. In addition to identifying factors that may limit a species' range, distribution models can identify new areas at risk of invasion and help guide management strategies to prevent further losses of biodiversity (GUISAN & THUILLER 2005).

The aim of our review is to examine the utility of distribution models for predicting the potential range of in-

troduced ant species and the potential consequences of climate change on their distribution. Specifically, after introducing the reader to the utility of species distribution models, and the different (correlative vs. mechanistic) approaches available, we review the literature on distribution models that assess changes in the geographic range of invasive ant species. We emphasize the results of studies that consider future scenarios of climate change to address the potential consequences of global warming on the current distribution of invasive ant species. In addition, we identify some limitations of distribution models and areas of future research required to understand the present-day and future consequences of climatic change on the distribution of ants.

Overview of species distribution modelling

Species distribution models have been widely used to assess the geographic dimensions of biological invasions under current climates, and also under scenarios of global warming (PETERSON 2003). Distribution models use both direct and indirect measures of species' characteristics, both ecological and physiological, to assess the total environmental range within which a species is able to survive and reproduce indefinitely. This environmental range represents the entire set of abiotic conditions – which correspond to environmental gradients along which an organism exhibits different tolerance ranges – that a species could occupy in the absence of biotic influences. Nevertheless, competition and other forms of biotic interactions may prevent species from occupying the whole environmental range of suitable conditions from simply an abiotic perspective (GILLER 1984). Moreover, the geographic distribution of a species is constrained not only by abiotic and biotic conditions, but also by its evolutionary capacity to adapt to new environmental conditions (SOBERÓN & PETERSON 2005).

Understanding the main drivers shaping the geographic range of a species is particularly important in the context of distribution modelling approaches (PULLIAM 2000). Some models correlate environmental abiotic variables influencing species' ecology with present-day observed distribution to identify areas suitable for the species (correlative approach, Fig. 1), while others use direct measures of individuals' mechanistic response to environmental conditions (eco-physiological and spatially-explicit spread mechanistic approaches, Fig. 1). Mechanistic approaches can additionally incorporate biotic interactions to predict the geographic distribution of the species (GUISAN & ZIMMERMANN 2000, SOBERÓN & PETERSON 2005). A detailed discussion on the main limitations affecting species distributional models, and also on the advantages and disadvantages of both correlative / mechanistic approaches, is extensively summarized in PEARSON & DAWSON (2003).

Coincident with the development of species distribution models, there has been an increasing awareness regarding the need to explicitly incorporate scale into ecological studies (LEVIN 1992). Species' distributional patterns are inherently scale-dependent, since the importance of different factors can vary considerably across scales (WIENS 1989, MACKAY & LINDENMAYER 2001, FARINA & al. 2005). Predicting a species' potential distribution requires reducing the multi-dimensional natural environment into a few scales due to our limited perceptual capabilities and technical constraints (LEVIN 1992). To select the most appropriate scale and factors for modelling the phenome-

non of study, several authors proposed a modelling framework where factors determining the distribution of a species operate in a hierarchical manner from global to local scales: at global scales climate appears to be the dominant factor determining species distribution, while at regional to local scales topography and land-use become more important. However, biotic interactions and microclimate factors shape species distribution at the finest scales (GUISAN & ZIMMERMANN 2000). This hierarchical framework relies on the interconnection between the different levels of a system, in which the higher levels constrain the lower levels and vice versa (PEARSON & DAWSON 2003). Thus, in the context of species distribution models, abiotic factors (such as climate and topography mainly) seem to be more influential at global and regional scales than biotic factors, which may occupy lower levels in the hierarchy and therefore become more limiting when higher level conditions are satisfied (WILLIS & WHITTAKER 2002).

From this perspective, the selection of the most appropriate spatial scale and modelling approach needs to take into consideration the purpose of the study to produce accurate estimations of the geographic dimensions of a species' ranges (LEVIN 1992). In this sense, several authors have identified correlative models as more appropriate at global, regional and landscape scales than mechanistic models, which seem to be more accurate at finer spatial scales (GUISAN & ZIMMERMANN 2000, RICHARDSON & al. 2004, HELMUTH & al. 2005).

Assessing change on the geographic distribution of invasive ants using species distribution models

Several studies have used species distribution models to predict the current distribution of invasive ant species, but few have assessed changes in their distribution associated with climate change. For the purpose of this paper (i.e., determine the utility of distribution models to anticipate changes in the distribution of invasive ants), we review approaches currently applied to predict the current and future geographic range of invasive ant species. We will distinguish between studies developed using a correlative niche modelling approach and those using a mechanistic modelling approach due to their different nature and scale of application, and also highlight those results that predict potential changes to the distribution of invasive species that may result from climate change.

Bioclimatic envelope models (correlative approach). Many statistical bioclimatic envelope models – also known as "habitat models", "climate-matching envelope", "ecological niche-based models", or other related names (PEARSON & DAWSON 2003, GUISAN & THUILLER 2005, SOBERÓN & PETERSON 2005) – have been used to predict the geographic distribution of invasive and non-invasive species under different scenarios of global climate change (HEIKKINEN & al. 2006). As already mentioned, all these approaches are based on correlations between occurrence data and environmental characteristics influencing species presence at present-day. Once developed, bioclimatic envelope models are then projected back onto future scenarios of climate change to identify areas presenting similar ecological conditions, and thus estimate changes on the potential geographic dimensions of the invasion in the future (Fig. 1). Several studies have adopted such a correlative

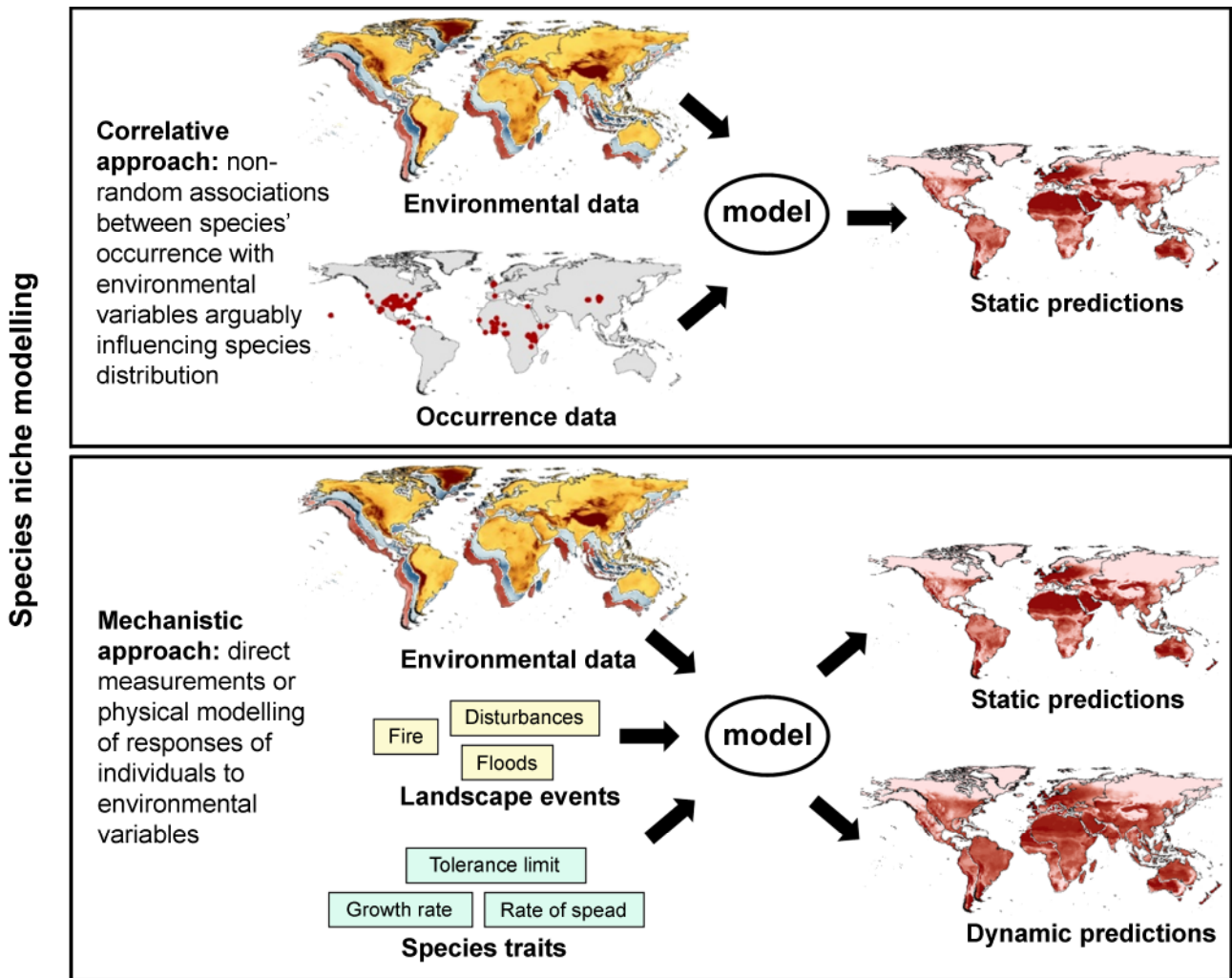


Fig. 1: Schemes of species distribution modelling showing differences between correlative *versus* mechanistic approaches.

approach to predict the current potential distribution of invasive ant species (PIMM & BARTELL 1980, CHARLES & al. 2001, HARTLEY & al. 2003, FITZPATRICK & WELTZIN 2005, HARTLEY & al. 2006, FITZPATRICK & al. 2007, WARD 2007, PETERSON & NAKAZAWA 2008, STEINER & al. 2008), but few have explicitly assessed potential geographic changes with global climate change (ZVALETA & ROYVAL 2002, ROURA-PASCUAL & al. 2004).

ZVALETA & ROYVAL (2002) examined the relationship between January mean minimum temperatures and red imported fire ant (*S. invicta*) occurrences to predict changes in the area of infestation for temperature increases of 1 - 4 °C, without linking it to any specific scenario of climate change. Their results indicate an increase in habitable areas in response to global warming: 62 % increase of the current distribution given a 3 °C rise in temperature, and 80 % given a 4 °C.

ROURA-PASCUAL & al. (2004) used data from the native range of the Argentine ant (*Linepithema humile*) to develop a model for predicting the worldwide potential distribution of this species under current and future climates. Under scenarios of climate change for 2050s, Argentine ants are expected to expand their environmental

range to higher northern and southern latitudes, and retract in the tropics at global spatial scales (Fig. 2). However, since the extent to which species are able to achieve large-scale migrations is still poorly understood and models did not take species' dispersal capacity into account, the impacts of climate change on invasive species at global scale remain uncertain to some extent (BROENNIMAN & al. 2006). Specific knowledge on the dispersal ability of *L. humile* to migrate would be necessary to improve the ecological realism of their predictions, by incorporating explicitly migration rates into the models (see for example SUAREZ & al. 2001).

Ecophysiology-based models (physiological mechanistic approach). When using correlative approaches to model a species' potential distribution, we are assessing those areas presenting suitable environmental conditions for the survival of the species based on correlations between locality data and environmental variables. In contrast with this correlative approach, ecophysiology-based models base their predictions on direct physiological measures of how a species responds, in terms of growth or tolerance for example, to specific abiotic conditions such as temperature and moisture (HELMUTH & al. 2005) (Fig. 1).

For ant invasions, PORTER (1988) developed a degree-day model for the red imported fire ant and determined that colony growth was maximal around 32 °C and ceased below 24 °C. STOKER & al. (1994) expanded on this work by providing the first mechanistic model to estimate population and colony growth of *Solenopsis invicta*, taking into consideration the different developmental stages. More recently, several authors have estimated the potential range expansion of *Solenopsis invicta* at both fine and coarse scales using ecophysiological models of colony growth and alate production based on soil temperatures (KILLION & GRANT 1995, KORZUKHIN & al. 2001, MORRISON & al. 2004, SUTHERST & MAYWALD 2005, XIONG & al. 2008).

Similarly, HARTLEY & LESTER (2003) constructed a degree-day model for colony growth of Argentine ants, based on development rates for different life-stages of the species in relation to temperature using laboratory data from NEWELL & BARBER (1913) and BENOIS (1973), to assess the geographic limits of the invasion in New Zealand. The same model was also applied to predict the range of *L. humile* in Hawaii (KRUSHELNYCKY & al. 2005), and in Catalonia (northeastern Iberian Peninsula) using new data on development rates (S. Abril, N. Roura-Pascual, J. Oliveras & C. Gómez, unpubl.).

However, few of these studies have assessed changes in the potential distribution of invasive ants in response to global climate change. Based on the literature available on factors determining the suitability of a given area for the survivorship of *Solenopsis invicta*, LEVIA & FROST (2004) assessed the potential expansion of the species under current and three scenarios of future climatic change in Oklahoma (USA). Instead of using a model to make the predictions, authors combined a series of suitability indicators in the form of GIS coverages (mean annual precipitation, consecutive days of a specific mean air temperature, and mean winter air temperature) to produce a series of suitability maps representing the potential range of the species. They found that three-quarters of Oklahoma is currently suitable for potential invasion of *S. invicta*, and it could increase between 26 % and 36 % under global warming.

Similarly, MORRISON & al. (2005) assessed the potential distribution of *S. invicta* in eastern USA over the next century under the Vegetation-Ecosystem Modelling and Analysis Project (VEMAP) climate change scenario, using the dynamic ecophysiological model developed by KORZUKHIN & al. (2001). This model functions with two time steps: the first simulating the effects of temperature on colony growth and mortality, and the second predicting the future geographic ranges based on estimated life-time alate production calibrated to current extreme limits of the *S. invicta* range (KORZUKHIN & al. 2001). Their predictions indicate that the habitable area for the species in the eastern United States may increase by 5 % within the next 40 - 50 years (a northward expansion of 33 ± 35 km), and by > 21 % (a northward expansion of 133 ± 68 km) in the latter half of the century (MORRISON & al. 2005).

Spatially-explicit spread models (spatial mechanistic approach). The capacity of a species to either persist or expand in response to climate change is not only constrained by physiological limits, but also by dispersal factors. When a species is incapable to physiologically adapt to new environmental conditions, the species will have to

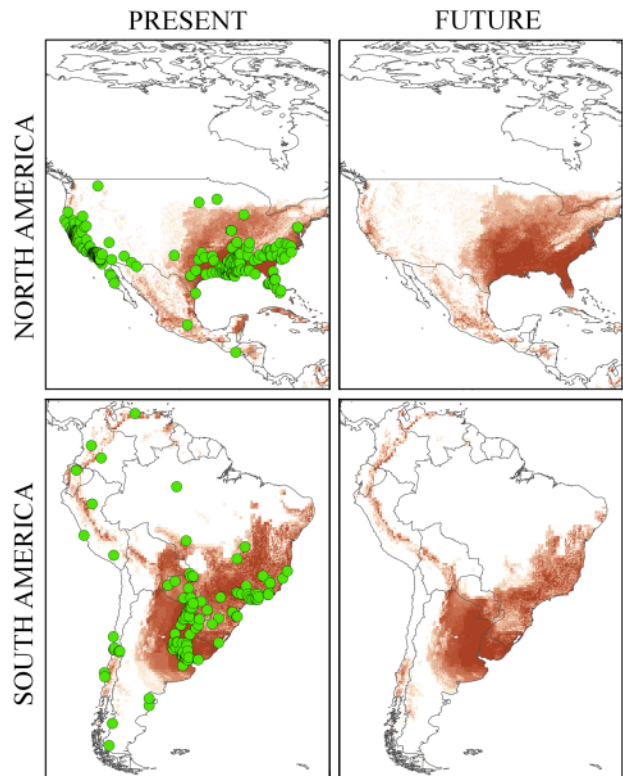


Fig. 2: Changes in the potential distributional area of the Argentine ant in North and South America according to present and 2050ies climatic conditions (extracted and modified from ROURA-PASCUAL & al. 2004). "Future" maps represent the averaged predictions of two scenarios of global climate change: HadCM3A2 and CGCM2A2 (IPCC 2007). Red darker shades indicate higher suitability areas for the species, and green dots indicate its present known distribution.

spread to new suitable conditions or restrict its distribution to those areas with a particular micro-environment to survive.

In order to understand and predict ant invasion spread patterns, spatially-oriented models taking into account the species dispersal mode are currently being developed (J.P. Pitt, S.P. Worner, A.V. Suarez, unpubl.). However, predicting the spread and direction of ant invasions is not an easy task because most species spread by multiple methods, such as diffusion like processes into neighbouring areas and through human-mediated jump dispersal (SUAREZ & al. 2001). We are currently unaware of any published study on invasive ants that makes use of spatially-explicit spread models to simulate the expansion of a species given current or future conditions associated with global climate change. Nevertheless, a modular and flexible spatially-explicit simulation model – so called Modular Dispersal in GIS, MdiG – can be used to, e.g., recreate the historical spread of *L. humile* in New Zealand, from the site of its initial introduction to its present-day distribution (J.P. Pitt, S.P. Worner, A.V. Suarez, unpubl.). The model is composed of two modules, each one simulating the diffusion and jump dispersion modes of the species. Although this study in progress does not take into consideration future changes on the distribution of the Argentine ant under global warming, these spatially-explicit spread mechanistic

models could potentially be applied to climate change analysis.

Limitations of species distribution models to predict changes on the potential distribution of invasive ant species

Regardless of the modelling approach, species distribution models present a series of inherent limitations to correctly predict changes in the potential distribution of a species with global climate change (DAVIS & al. 1998, PEARSON & DAWSON 2003, GUISAN & THULLER 2005). As already mentioned, the geographic range of a species is the result of the complex relationship between its ecology and evolutionary history (PULLIAM 2000, SOBERÓN & PETERSON 2005, WIENS & GRAHAM 2005), determined by different factors and processes acting at different scales (WIENS 1989). In this section, therefore, we present the advantages and constraints of using distribution models to anticipate changes in the distribution of invasive ants grouped in five categories: methodological aspects, abiotic conditions, biotic interactions, dispersal capacity, and adaptability of the species.

Methodological aspects. Among the factors affecting the performance of species distribution models, there is the modelling technique in itself. For the correlative approach, in a study comparing the performance of a wide range of modelling methods, ELITH & al. (2006) encountered differences in prediction performance depending on the technique and training data used to construct the model. Besides the increasing number of studies devoted to assess the distributional range of species by means of correlative approaches in the last years, a unique and perfect technique does not exist yet. Authors select the most appropriate modelling approach taking into account the question under study, the availability of data, and / or their technical skills.

Mechanistic approaches, however, are not exempt of limitations. Mechanistic models simulating the process under study as much close as possible to the reality will only produce realistic results if the data used to calibrate them is accurate. The incorporation of more details into a model does not necessarily improve the quality of the final predictions (KORZUKHIN & al. 2001). In this sense, HARTLEY & LESTER (2003) indicate that ecophysiological-based models considering only the effect of temperature upon individual development rates may underestimate many other temperature-dependent processes that are also important in determining colony growth and survival, such as oviposition behavior.

Independent of the adopted modelling approach, however, data quality is the ultimate and most important constraint to develop accurate distribution models. If the data is accurate and appropriate to address the question under study, models should be able to produce reliable estimates of the geographic range of the species under both present and future climatic conditions.

Abiotic conditions. Accuracy is not only necessary in species occurrence data, but also in the abiotic conditions used to estimate the distribution of the species. Parameters considered in distribution models may not necessarily be the most physiologically relevant, if those having the greatest influence are not available, or difficult to measure in the field or experimentally (HELMUTH & al. 2005). In this sense, HELMUTH & al. (2005) argue that for biophysical

methods to translate into large-scale indicators of environmental suitability, physiologically relevant parameters for individual organisms need to be incorporated. Such an understanding is critical to enable large-scale predictions of climate change on biodiversity, as FITZPATRICK & al. (2007) and PETERSON & NAKAZAWA (2008) have demonstrated in assessing the potential distribution of *Solenopsis* spp. under current climates.

Although potentially difficult to obtain for large spatial scales, the addition of key environmental variables such as soil temperature, soil moisture, and degree-days (as the total amount of temperature required for an organism to develop its life cycle) would significantly improve the accuracy of our final predictions. As an example, HARTLEY & LESTER (2003) question the accuracy of using air temperatures from meteorological stations as relative indicators of nest temperatures in their degree-day model predicting development stages of Argentine ants.

An additional constraint to species distribution models is that patterns due to microhabitat heterogeneity are not detectable at certain spatial scales, and small variations in environmental relevant parameters over small distances are not taken into consideration (HELMUTH & HOFMANN 2001, MORRISON & al. 2005, MENKE & al. 2007). In this sense, although models might also predict that species will not be able to survive in some localities at certain spatial scales, species are known to survive unsuitable conditions near urban habitation or greenhouses holding the appropriate range of temperatures and precipitation (SUAREZ & al. 2001, CALLCOTT & COLLINS 1996). However, in non-urban situations climate will probably be the most important long-term limiting factor (HARTLEY & LESTER 2003).

Finally, when assessing future changes in the geographic distribution of species, we need to take into consideration that climate change does not only produce an increase in global temperature worldwide; rather it involves a set of seasonal and geographic patterns of several climatic and habitat constraints (WALTHER 2004, HELMUTH & al. 2005, BOTES & al. 2006, SUTHERST & al. 2007). For example, Argentine ant nest site suitability is known to be influenced by climatic conditions and water (HOLWAY 1998), so a better understanding of how precipitation and water courses will change in the future is required to predict the real effects of global warming on its invasion pattern. Riparian areas, natural corridors that favor the spread of the Argentine ant into novel environments (HOLWAY 1998), have been identified as extremely vulnerable and may experience large biodiversity losses (SALA & al. 2000).

Biotic interactions. A factor potentially limiting the accuracy of model predictions based on abiotic factors alone is biotic interactions among invasive ants and other species (including interspecific competition, predation, mutualisms with honey-dew excreting hemipterans, parasitism, etc.), which are recognized as important forces shaping the distribution of ant populations (HÖLLDOBLER & WILSON 1990). However, when the introduced species outcompetes resident species, the main factors limiting the spread of the invasion are likely to be abiotic rather than biotic (MORRISON & al. 2005). This appears to be the case with *Linepithema humile* in the Mediterranean basin and in California, where other ants do not seem to limit their distribution (HOLWAY 1998, ROURA-PASCUAL & al. 2004). However, its distribution in its native range in South Am-

erica appears constrained by other ant species, including congeners and other highly competitive ants many of which are also successful invaders elsewhere (Fig. 2) (WILD 2004, LEBRUN & al. 2007). A similar situation may occur with *S. invicta*, which is more abundant in its introduced range in the southeastern United States than in its South America homeland (BUREN 1983, PORTER & al. 1997). However, in addition to biotic interactions with the diverse and aggressive ant fauna in South America, fire ants have also escaped natural enemies in the form of phorid fly parasitoids which can influence foraging behavior and colony growth (PORTER & al. 1997, MORRISON 1999). Nevertheless, the role that such enemies might finally play as bio-control agents in limiting the distribution of ant species in invaded areas in the future remains uncertain (HENNE & al. 2007). Interestingly, the only ant thought to have eradicated Argentine ants from parts of the southeastern U.S. is the red imported fire ant (WILSON & BROWN 1957).

When biotic interactions are likely to influence final predictions, assessing the species' geographical range must be done with caution and taking into account all these different biotic interactions. This is especially true when assessing the future distribution of invasive species, since biotic interactions are expected to change considerably and therefore become more complex in the future with global warming (DAVIS & al. 1998). To overcome these limitations, SUTHERST & al. (2007) suggest using more complex mechanistic models and the need of data from experimental studies.

Dispersal capacity. As indicated in previous paragraphs, the effects of global warming on species distributions are known not to be the consequence of simple species temperature responses, but the results of multiple additional factors such as complex species interactions and species dispersal (DAVIS & al. 1998). In this sense, one of the major constraints to anticipate changes in species' distributions may be related to our ability to model their dispersal capacity. Dispersion, however, is not only determined by the biological characteristics of the species (dispersal mode). Other factors are likely to influence species dispersal capacity: history of the invasion (time of residence and propagule pressure, WILSON & al. 2007), landscape heterogeneity (geographic barriers and habitat suitability, J.P. Pitt, S.P. Worner, A.V. Suarez, unpubl.), and configuration of metapopulations (population interdependencies, HANSKI 2004). All these dispersal related factors, coupled with climate change and interactions with other species, need to be incorporated into models to produce accurate predictions of the potential consequences of global warming.

However, developing a model including dispersal-related factors is not trivial, and requires an important amount of data and an extraordinary knowledge on the invasion process to increase the realism of final predictions. Considering only the dispersal mode, predicting the geographic range of invasive ants might be quite complicated when the most important factor governing its distribution is not the natural rate of spread, but human-assisted jump-dispersal (SUAREZ & al. 2001, WARD & al. 2006). Although spatially-explicit spread models make an effort to incorporate these long-distance events (J.P. Pitt, S.P. Worner, A.V. Suarez, unpubl.), the dimensions and final localization of them is quite – if not totally – impossible to predict. Ultimately, this may lead to the general pattern that

models often under-predict an invader's rate of spread (HASTINGS & al. 2005).

A similar situation happens when the present-day distribution of the invasive ants under study are at an early stage of the invasion process. This non-equilibrium situation is a drawback for most distribution models, since these implicitly assume a state of equilibrium between species and their environment (GUISAN & ZIMMERMANN 2000). As such, models derived from this data may underestimate the geographic range of the species (GUISAN & ZIMMERMANN 2000, PETERSON 2005). However, non realistic distributions may also result from not including landscape configuration and dispersal (source-sink) dynamics between populations into the models (HANSKI 2004). Although both factors are known to influence the distribution of ant invasions by facilitating the spread of individuals between neighboring areas or allowing species to maintain populations outside their physiological optima (HELLER & al. 2006, MENKE & al. 2007), modelling efforts have not yet incorporated such information to increase the realism of their predictions.

Adaptability of the species. Distribution models assume that a species' capability of adapting to new environments occurs at long (evolutionary) temporal scales, thus the environmental conditions that predict a species range in different geographic areas and under future climate changes should be similar or identical (niche conservatism) (PETERSON & al. 1999). However, adjustments to new conditions by means of phenotypic plasticity and/or rapid evolutionary changes in tolerance to the local environmental conditions, which could facilitate the persistence of species outside their current optimal environmental conditions can certainly occur (HAIRSTON & al. 2005), and thus reduce the predictive capacity of distribution models (HELMUTH & al. 2005).

Using a correlative modelling approach to assess changes in tolerance to environmental conditions between native and introduced populations of the Argentine ant, ROURAPASCUAL & al. (2006) did not find significant differences at global and regional scales. However, due to the lack of studies at local scales searching for changes in Argentine ant environmental tolerances, we cannot underestimate their influence. In fact, PHILLIPS & al. (1996) found that western populations of *Solenopsis invicta* in North America have adapted to more xeric conditions. This finding is also corroborated by FITZPATRICK & al. (2007), which used a correlative model to test whether *S. invicta* occupies similar environments in its native and introduced ranges. Their results indicate that *S. invicta* in North America occupies colder, drier and more seasonal environments than in its native range (South America), and that fire ants initially invaded environments similar to those found within their native range and then spread into harsher environments not included in their native distribution. However, in relation to this study, PETERSON & NAKAZAWA (2008) suggested that these differences do not necessarily correspond to biological explanations, but to methodological considerations such as the selection of the environmental data set used to calibrate the model.

Nevertheless, besides the potential climate-driven phenotypic responses of invasive ant populations to new environmental conditions, the underlying mechanisms responsible of these changes remain largely uncertain. While phen-

otypic plasticity permits species to respond to new local environmental conditions without altering their genetic structure, microevolutionary adaptation may be required for persistence in the face of changing climates (GIENAPP & al. 2008). In this sense, HOFFMANN & al. (2003) suggest that generalist species with broader distribution present a higher potential for genetic adaptation than species from restricted habitats. However, up to date, no study on genetic adaptability of ant species to climate change has been conducted and conclusions on this issue are uniquely speculative.

In addition to these aforementioned reservations, there are some further limitations depending on the approach adopted to model the geographic distribution of invasive ants (GUISAN & ZIMMERMANN 2000, PEARSON & DAWSON 2003). The major criticism of the correlative approach is that species distribution may not be in equilibrium with its environment (as happens with most invasive species) due to biotic interactions, dispersal characteristics, and human management of the landscape, and thus correlative models may not predict the full range of areas suitable for the species. Contrarily, since mechanistic models do not assume equilibrium or a relationship between species occurrence and environmental data, models based on physiological restrictions to species ranges are expected to identify the absolute environmental limits more precisely. However, mechanistic models have other limitations (such as not providing information on the current distribution of a species; also, individuals of a species may show different tolerance ranges; finally, rapid evolutionary changes may modify the environmental range) that restrict their predictive capacity to estimate the species' geographic distribution (GUISAN & ZIMMERMANN 2000, PEARSON & DAWSON 2003, SOBERÓN & PETERSON 2005).

Future studies

In light of current research and the limitations of species distribution models presented above, future research efforts on this topic (i.e., predict potential changes in the distribution of invasive ant species) should basically focus on three main aspects: (1) improve the current knowledge on the spatial distribution of introduced ants, (2) identify the main factors responsible of future changes in the distribution of ant species, and (3) improve the predictive capacity of species distribution models by taking into account additional factors.

First, given the often severe consequences of invasive ants, there is an urgent need to set up worldwide distributional database on invasive ant species, which could be updated and continuously maintained to notify new and / or predicted occurrences (both presence and absence) of the species. This would help to develop a monitoring network to facilitate the prevention of new infestations or at least detect them immediately after establishment when eradication may still be possible. This could be readily accomplished for some species, such as the Argentine ant and the red imported fire ant, as most of the current occurrence data have already been summarized in a few works (e.g., ROURA-PASCUAL & al. 2004, FITZPATRICK & al. 2007).

Second, more studies determining the influence of multiple factors (both abiotic and biotic factors, dispersal, and phenotypic and genotypic changes) governing the spread of invasive ant species are needed in different areas and across a variety of spatial scales (especially at small scales). In

general, the most interesting topics at broader scales include understanding the genetic distribution of invasive ant populations (to reconstruct the historical pathways of invasion and to determine possible changes in tolerance to environmental conditions after introductions, and the population-specific mechanisms of dispersal) and understanding the biotic factors that determine range limits in each introduced area. Likewise, at local scales, more single-site studies at the invasion front (by establishing a multi-scale nested sampling strategy along the main environmental gradients or a long-term monitoring of an invasion focus, e.g., SANDERS & al. 2001) could significantly contribute to defining the invasive pattern of ant species in detail.

Finally, from the modelling perspective, data on biotic interactions and species adaptability to new climatic conditions should be incorporated into distribution models to determine the potential distribution of the species under future climates (HELMUTH & al. 2005, BALANYA & al. 2006). In addition, the adoption of a mechanistic approach combining eco-physiological data with the species' dispersal capabilities would allow to test several hypotheses about its past and future expansion. The use of such spatially-explicit spread models incorporating species populations' characteristics and environmental variability would allow tracking the migration and gene flow among populations, and thereby determining the ecological and genetic viability of ant species in introduced areas. The combination of distributional models and landscape ecology, taking into account data on population adaptability to changing environments, is thus required to produce more realistic distributional patterns of ant invasions under climate change (HELMUTH & al. 2005).

Nevertheless, one of the main objectives underlying the motivation for distributional studies of invasive species is to elucidate the geographic dimension of the process, which is required to establish efficient management strategies for preventing further expansions of an invasion. As such, considerable efforts should be to identify those human activities susceptible to transporting propagules of invasive ants over long and short distances, from the native area or from another introduced population. Effectively controlling these secondary jump-dispersal events is crucial for avoiding the posterior spread of most invasive ant species into natural habitats and ecosystems (KRUSHELNYCKY & al. 2005), which seems to be highly probable in all areas neighboring human settlements (CARPINTERO & al. 2004). All measures aimed at preventing and controlling ant invasions, however, need to be integrated into a global strategy acting across several temporal and spatial scales, such as those suggested by MCNEELY & al. (2001). But global and regional initiatives will not successfully manage the complex phenomenon of invasions without the widespread support of all citizens (VITOUSEK & al. 1997), who can contribute to preventing or mitigating them by becoming more aware of those local actions that favor the spread of invasive species.

Conclusions

Understanding the current and potential future geographic distribution of ant invasions is extremely important for the establishment of efficient management strategies. In the absence of detailed occurrence data, species distribution models can help us to estimate the potential distribution of in-

vasive species. However, the above-mentioned constraints need to be considered when interpreting final results, especially when predicting the impacts of climate change on a species distribution (PEARSON & DAWSON 2003) or when extrapolating data among different regions (THULLER & al. 2004). There is no perfect modelling approach that captures the complexity of natural environments or the many processes that determine a species' geographic distribution, but the choice of the most appropriate technique in each specific modelling context may reduce inaccurate results (ELITH & al. 2006).

In this sense, we encourage the use of correlative approaches to assess the suitability of large areas or regions for the spread of introduced ants based on abiotic factors (i.e., climatic and topographic). However, to determine the present-day distribution of invasive ant species or geographic changes with global warming at smaller spatial scales, mechanistic models including biotic interactions (if possible) and dispersal processes might provide a more precise and realistic overview of the expansion. Indeed, this is in concordance with the hierarchical frameworks of GUISAN & ZIMMERMANN (2000) and PEARSON & DAWSON (2003), who suggest that biotic interactions tend to affect distribution models at fine scales (WILLIS & WHITTAKER 2002).

Despite the limitations of correlative and mechanistic models discussed above, the importance of species distribution models should not be underestimated. When applied at an appropriate scale and correctly interpreted taking into account their inherent limitations, distribution models provide a valuable assessment of the current geographic dimensions of species' distributions. Moreover, they allow us to predict changes in species' distributions under future scenarios of climate and anticipate the establishment of invasive species in new geographic areas. This information is essential for prioritizing monitoring efforts to prevent new invasions.

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Zusammenfassung

In den letzten Jahrzehnten rückten Artenverbreitungsmodelle, welche die geographische Verbreitung von invasiven Arten vorhersagen, zunehmend ins Rampenlicht. Dieser Zugang ist sehr hilfreich für das Ermitteln des Potenzials zusätzlicher Ausbreitung in schon besiedelten Gebieten sowie für die Identifizierung von potentiell besiedelbaren aber bisher noch unbesiedelten Regionen. Mit der zunehmenden Verfügbarkeit von klimatischen Zukunftsszenarien haben Wissenschaftler zusätzlich die einzigartige Möglichkeit, Veränderungen in der Verbreitung von Arten, die aus der globalen Klimaerwärmung resultieren, zu berechnen. Wie exakt Artenverbreitungsmodelle in der Vorhersage von biogeographischen Veränderungen in Folge der globalen Klimaerwärmung sind, bedarf allerdings eingehender Evaluierung. Unsicherheiten rühren teilweise aus methodenver-

hafteten Problemen der Artenverbreitungsmodelle. Beispielsweise beziehen die Modelle biotische Interaktionen, welche die Verbreitung von Arten beeinflussen können, nicht ein. Weiters können die abiotischen Faktoren, die einbezogen werden, nicht die einzigen sein, die für eine präzise Vorhersage der geographischen Verbreitung nötig sind. Wir fassen Arbeiten zusammen, die zur Vorhersage der Verbreitung von invasiven Ameisen entweder den korrelativen oder den mechanistischen Modellansatz verwendet haben. Unser Ziel ist dabei einerseits eine Standortbestimmung des Forschungsgebiets und andererseits das Hinweisen auf Bereiche, deren weiterführende Bearbeitung unerlässlich ist, um aktuelle und zukünftige Auswirkungen der globalen Erwärmung auf die Verbreitung invasiver Ameisen grundlegend zu durchdringen.

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