



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

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

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

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

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

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Paper submitted April 30, 2012; revised manuscript accepted February 20, 2013.

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

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

Introduction

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

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

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

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

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

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

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

Methods

Case Study

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

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

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

Species Distribution Data

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

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

Climatic Predictors

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

We sourced future climatic data from the 4th Intergovernmental Panel on Climate Change (IPCC) assessment report (GIEC 2007). The data set provided by the IPCC consisted of projections that had been calibrated and statistically downscaled with the WorldClim data for current conditions; therefore, the projections can be compared. To consider a range of possible future climates, we used downscaled climate data from 3 global circulation models (GCMs): CCCMA-GCM2 model, CSIRO-MK2 model, and HCCPR-HADCM3 model (GIEC 2007). Similarly, we used the 2 extreme Special Report on CO₂ Emission Scenarios (SRES): the optimistic B2a and pessimistic A2a scenarios. We used a spatial resolution of 10 arcmin (approximately 18.5 × 18.5 km pixel) because our aim was to make global projections. Predictions made on the basis of coarser resolutions are more likely to be controlled by climatic predictors, whereas fine-scale, patchy distributions at a smaller scale are more likely to be determined by microtopographic variations or habitat fragmentation (Guisan & Thuiller 2005).

Ecological Niche Modeling

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

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

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

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

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

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

A clear limitation of modeling is that outputs depend on the specifically chosen input settings, in this instance the algorithms, global climate models, and scenarios of human development. To minimize potential resulting variation, we conducted consensual forecasts (Araújo & New 2007) of combined models with the 5 different modeling techniques above with each of 3 climate models (GCMs) and 2 CO₂ emission scenarios. The purpose of consensual forecasts is to separate the signal from the noise associated with the errors and uncertainties of individual models by superposing the maps that are based on individual model outputs. Areas where these individual maps overlap are considered areas of consensual prediction (Araújo & New 2007). This consensus forecast is different from averaging the individual projections because the area pre-

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

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

We generated the consensus model with all 30 individual projections, each was based on a different combination of CO₂ scenario × GCM × modeling technique, and each yielded a consensus projection for one particular point in time. Consequently, we obtained a single value per consensus model, which we illustrated in the form of histograms. But because the underlying idea of consensus models is to incorporate the variation, there cannot be error bars of the variation between single models in the figures.

Model Validation

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

Assessing Climatically Suitable Areas

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

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

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

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

Results

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

Current Suitable Climatic Range

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

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

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

Quantitative Changes Following Climate Change

Changes in suitable areas were markedly different for the 2 species, both globally and among regions (Fig. 1). For *M. destructor*, the 2080 projection of land area with suitable climate increased by 35.8% globally, contrasting with a negligible change of suitable area for *M. rubra* (0.05% increase). For *M. destructor*, the potential distribution increased 6,614,046 km² in Africa, 3,902,005 km² in Asia, 2,471,088 km² in South America, 1,116,955 km² in Oceania, 523,239 km² in North America, and 111,314 km² in Europe (Fig. 3a). For *M. rubra*, climatically suitable area increased only in North America (3,431,359 km² increase) and in Europe (1,524,109 km² increase) and decreased in Asia by 2,565,870 km², in Africa by 533,266 km² in South America by 475,509 km², and in Oceania by 223,057 km² (Fig. 3b).

Qualitative Changes Following Climate Change

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

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

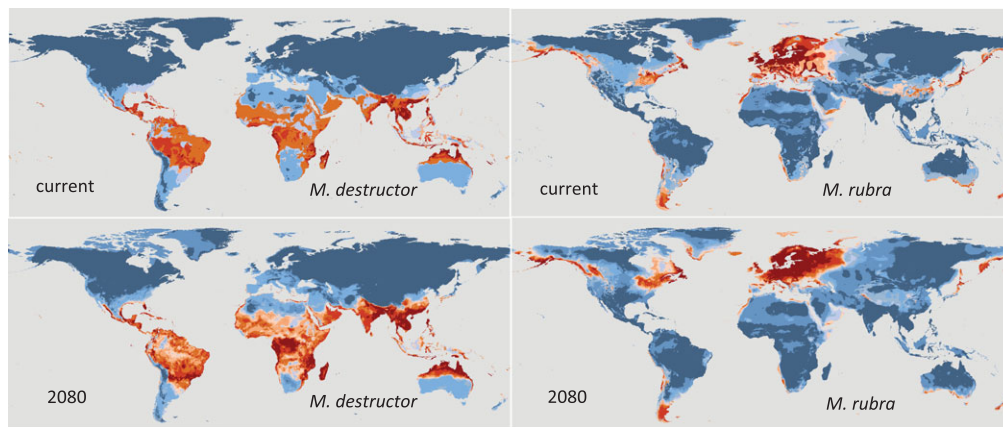


Figure 1. Results of consensus models of suitable climatic range for the invasive ants *M. destructor* and *M. rubra* under current climatic conditions and in 2080 (following global climate change) (reds, favorable areas from low climatic suitability [light rose, 0.5–0.6] to excellent climatic suitability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

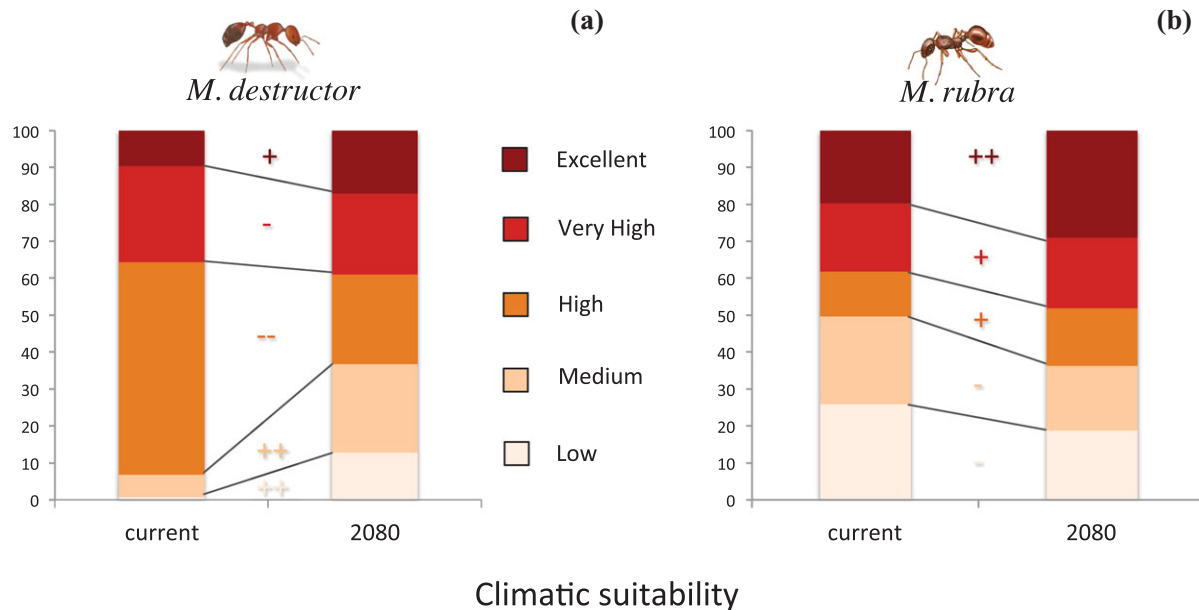


Figure 2. Distribution of climatically suitable areas for (a) *M. destructor* and (b) *M. rubra* among the geographic regions under current and future climatic conditions.

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

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

Discussion

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

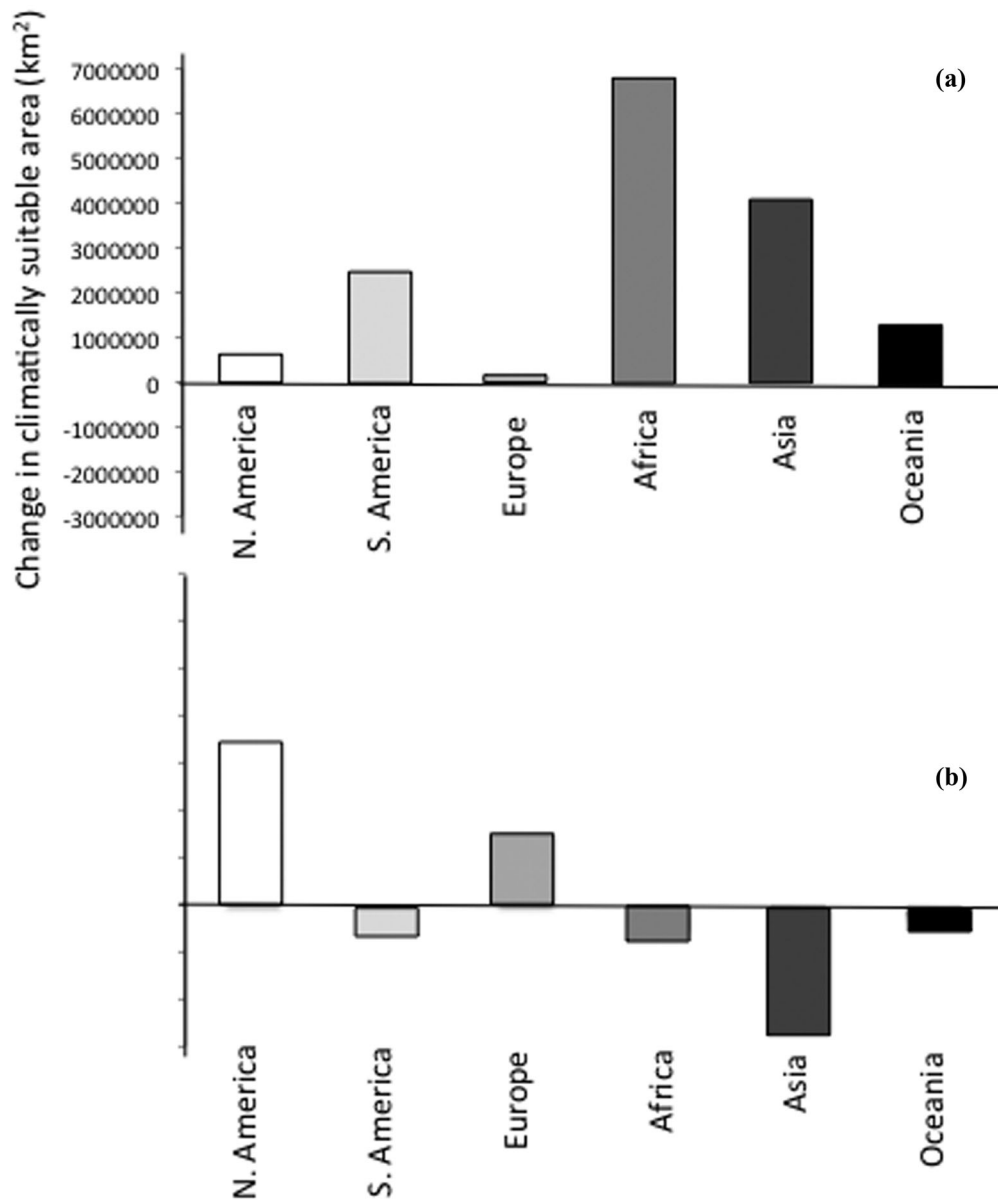


Figure 3. Changes in the amount of climatically suitable area for (a) *M. destructor* and (b) *M. rubra* across regions relative to the area that is currently climatically suitable. As the underlying idea of consensus models is to incorporate the variation, there cannot be error bars of the variation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

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

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

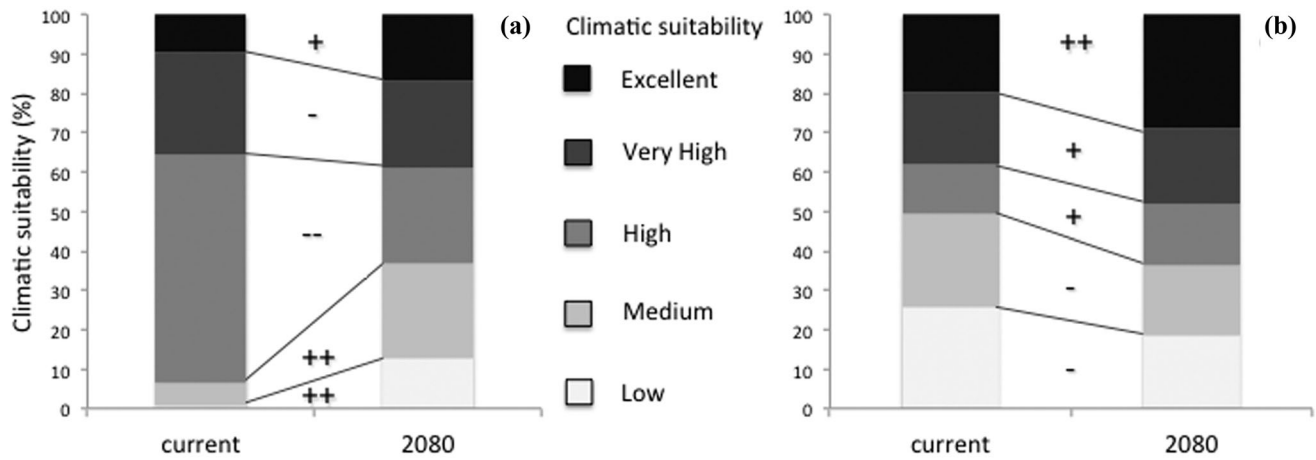


Figure 4. Changes in climate suitability classes (excellent to low as defined in Fig. 1) for (a) *M. destructor* and (b) *M. rubra* following climate change (+ and -, changes of <10%; ++ and --, changes of >10%).

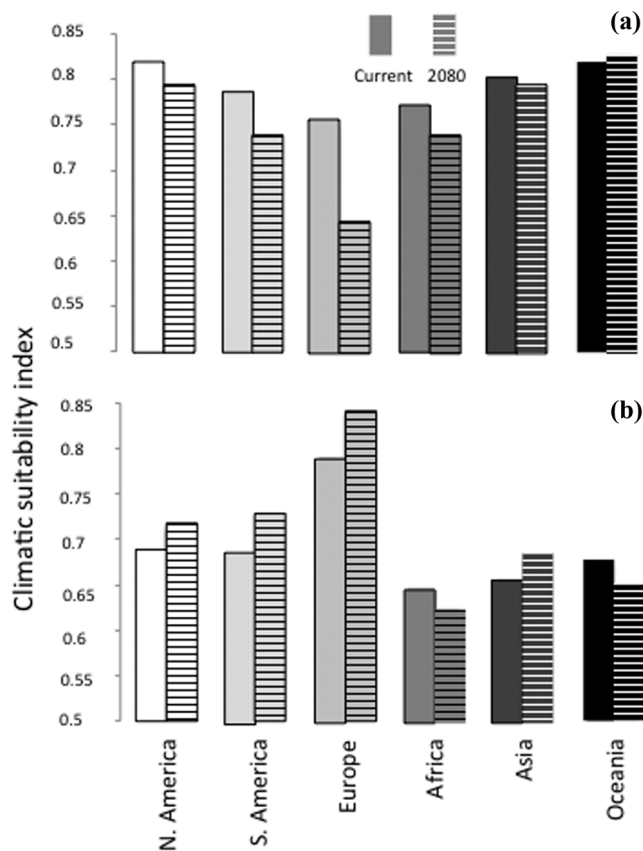


Figure 5. Changes in the climatic suitability index (i.e., quality) in climatically suitable areas across regions following climate change for (a) *M. destructor* and (b) *M. rubra*.

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

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

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

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

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

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

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

Acknowledgments

We thank B.D. Hoffmann for his helpful comments that improved the readability of the paper and for checking the species occurrence records and 2 anonymous referees for their help in improving an earlier version of this manuscript. This paper was supported by Région Ile-de-France (03-2010/GV-DIM ASTREA) and Agence Nationale de la Recherche (2009 PEXT 010 01) grants.

Supporting Information

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

Literature Cited

- Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* **22**:42–47.
- Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modelling. *Ecology* **93**:1527–1539.
- Bakkenes, M., J. R. M. Alkemade, F. Ihle, R. Leemans, and J. B. Latour. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* **8**:390–407.
- Beaumont, L. J., R. V. Gallagher, W. Thuiller, P. O. Downey, M. R. Leishman, and L. Hughes. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions* **15**:409–420.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* **15**:365–377.
- Bertelsmeier, C., G. M. Luque, and F. Courchamp. 2013. Global warming may freeze the invasion of big-headed ants. *Biological Invasions* DOI: 10.1007/s10530-012-0390-y.
- Bottrill, M. C., et al. 2008. Is conservation triage just smart decision making? *Trends in Ecology & Evolution* **23**:649–654.
- Broennimann, O., W. Thuiller, G. Hughes, G. U. Y. F. Midgley, J. M. R. Alkemade, and A. Guisan. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology* **12**:1079–1093.
- Chebib, A., et al. 2012. Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. *Ecology Letters* DOI: j.1461-0248.2012.01764.x.
- Cristianini, N., and B. Schölkopf. 2002. Support vector machines and kernel methods, the new generation of learning machines. *AI Magazine* **23**:31–41.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* **81**:3178–3192.
- Elith, J., C. Graham, R. Anderson, and M. Dudik. 2006. Novel methods improve prediction of species distributions from occurrence data. *Ecography* **29**:129–151.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38–49.
- Fokuhl, G., J. Heinze, and P. Poschod. 2007. Colony growth in *Myrmica rubra* with supplementation of myrmecochorous seeds. *Ecological Research* **22**:845–847.
- Franklin, J. 2009. Mapping species distributions – spatial inference and prediction. *Ecology, biodiversity and conservation series*. Cambridge University Press, Cambridge, United Kingdom.
- GIEC (Group of International Experts on Climate Change). 2007. Climate change 2007: synthesis report. An Assessment of the Intergovernmental Panel on Climate Change. GIEC, Geneva.
- Groden, E., F. A. Drummond, J. Garnas, and A. Franceour. 2005. Distribution of an invasive ant, *Myrmica rubra* (Hymenoptera: Formicidae), in Maine. *Journal of Economic Entomology* **98**:1774–1784.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**:993–1009.
- Guo, Q., M. Kelly, and C. Graham. 2005. Support vector machines for predicting distribution of sudden oak death in California. *Ecological Modelling* **182**:75–90.
- Guo, Q. H., and Y. Liu. 2010. ModEco: an integrated software package for ecological niche modeling. *Ecography* **33**:637–642.
- Guo, Q., D. F. Sax, H. Qian, and R. Early. 2011. Latitudinal shifts of introduced species: possible causes and implications. *Biological Invasions* **14**:547–556.
- Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovett, D. Scott, and F. I. Woodward. 2002. Conservation of biodiversity in a changing climate. *Conservation Biology* **16**:264–268.

- Harris, R., et al. 2005. Invasive ant pest risk assessment project for biosecurity New Zealand. Report BAH/35/2004. Landcare Research, Lincoln, New Zealand.
- Harris, R. J., and J. Rees. 2004. Ant distribution database. Landcare Research, Lincoln, New Zealand. Available from www.landcareresearch.co.nz/research/biocons/invertebrates/ants/distribution (accessed April 2011).
- Hastie, T. J., R. Tibshirani, and J. Friedman. 2001. The elements of statistical learning: data mining, inference and prediction. 2nd edition. Springer Verlag, New York.
- Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. *Conservation Biology* **22**:534–543.
- Hewitt, N., N. Klenk, A. L. Smith, D. R. Bazely, N. Yan, S. Wood, J. I. MacLellan, C. Lipsig-Mumme, and I. Henriques. 2011. Taking stock of the assisted migration debate. *Biological Conservation* **144**:2560–2572.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**:1965–1978.
- Hijmans, R. J., M. Cruz, and E. Rojas. 2001. Computer tools for spatial analysis of plant genetic resources data: 1. DIVA-GIS. *Genetic Resources Newsletter* **127**:15–19.
- IUCN (International Union for Conservation of Nature) SSC (Species Survival Commission) Invasive Species Specialist Group. 2012. Global invasive species database. IUCN, Gland, Switzerland. Available from <http://www.issg.org/database> (accessed January 2012).
- Jimenez-Valverde, A., A. T. Peterson, J. Soberon, J. M. Overton, P. Aragon, and J. M. Lobo. 2011. Use of niche models in invasive species risk assessments. *Biological Invasions* **13**:2785–2797.
- Keith, D. A., H. R. Akcakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araújo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* **4**:560–563.
- Klamt, M., R. Thompson, and J. Davis. 2011. Early response of the platypus to climate warming. *Global Change Biology* **17**:3011–3018.
- Maravelias, C., J. Haralabous, and C. Papaconstantinou. 2003. Predicting demersal fish species distributions in the Mediterranean Sea using artificial neural networks. *Marine Ecology Progress Series* **255**:240–258.
- Nenzén, H. K., and M. B. Araújo. 2011. Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* **222**:3346–3354.
- Normand, S., U. A. Treier, C. Randin, P. Vittoz, A. Guisan, and J.-C. Svenning. 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography* **18**:437–449.
- O'Donnell, J., R. V. Gallagher, P. D. Wilson, P. O. Downey, L. Hughes, and M. R. Leishman. 2011. Invasion hotspots for non-native plants in Australia under current and future climates. *Global Change Biology* **18**:617–629.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* **133**:225–245.
- Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. Niche dynamics in space and time. *Trends in Ecology & Evolution* **23**:149–158.
- Petitpierre, B., C. Kueffer, O. Broennimann, C. Randin, C. Daehler, and A. Guisan. 2012. Climatic niche shifts are rare among terrestrial plant invaders. *Science* **335**:1344–1348.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**:231–259.
- Root, B. A., J. T. Price, and K. Hall. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**:47–60.
- Roura-Pascual, N., L. Brotons, A. T. Peterson, and W. Thuiller. 2009. Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. *Biological Invasions* **11**:1017–1031.
- Sinclair, S., M. White and G. R. Newell. 2010. How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society* **15**(1):8.
- Summers, D. M., B. A. Bryan, N. D. Crossman, and W. S. Meyer. 2012. Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. *Global Change Biology* **18**:2335–2348.
- Thomas, C. D., et al. 2004. Extinction risk from climate change. *Nature* **427**:145–148.
- von Aesch, L., and D. Cherix. 2005. Introduced ant species and mechanisms of competition on Floreana Island (Galapagos, Ecuador) (Hymenoptera: Formicidae). *Sociobiology* **45**:463–481.
- Walther, G., et al. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* **24**:686–693.
- Warren, D. L. 2012. In defense of “niche modeling.” *Trends in Ecology & Evolution* **27**:497–500.
- Wetterer, J. K. 2009. Worldwide spread of the destroyer ant, *Monomorium destructor* (Hymenoptera: Formicidae). *Myrmecological News* **12**:97–108.

