

Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula

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Abstract Invasive species are known to influence the structure and function of invaded ecological communities, and preventive measures appear to be the most efficient means of controlling these effects. However, management of biological invasions requires use of adequate tools to understand and predict invasion patterns in recently introduced areas. The present study: (1) estimates the potential geographic distribution and ecological requirements of the Argentine ant (*Linepithema humile* Mayr), one of the most

conspicuous invasive species throughout the world, in the Iberian Peninsula using ecological niche modeling, and (2) provides new insights into the process of selection of consensual areas among predictions from several modeling methodologies. Ecological niche models were developed using 5 modeling techniques: generalized linear models (GLM), generalized additive models (GAM), generalized boosted models (GBM), Genetic Algorithm for Rule-Set Prediction (GARP), and Maximum Entropy (Maxent). Models for the eastern and western portions of the Iberian Peninsula were built using subsets of occurrence and environmental data to investigate the potential for ecological niche differences between the invading populations. Our results indicate geographic differences between predictions of different approaches, and the utility of ensemble predictions in identifying areas of uncertainty regarding the species' invasive potential. More generally, our models predict coastal areas and major river corridors as highly suitable for Argentine ants, and indicate that western and eastern Iberian Peninsula populations occupy similar environmental conditions.

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Introduction

Rates of species' introductions are increasing globally as a consequence of broadening human movements (Vitousek et al. 1997). This invasive presence frequently has negative influences on native communities and ecosystems, with consequences such as species loss, food web reorganization, community simplification, and changes in disturbance regimes (Chapin et al. 2000; Mack et al. 2000). As such, techniques for modeling species' potential distributions could support pro-active strategies to avoid the introduction or to guide screening to impede establishment of invasive alien species (Peterson 2003; Drake and Lodge 2006).

A highly successful invasive species is the Argentine ant (*Linepithema humile*). Native to the Río de la Plata region in South America (Tsutsui et al. 2001; Wild 2004), Argentine ants are now established in many Mediterranean-type and subtropical areas worldwide (Suarez et al. 2001). With the development of global trade, Argentine ants have been transported on a large scale to new areas associated with humans (Suarez et al. 2001; Ward et al. 2005), from where they invade natural habitats, causing severe ecologic and economic impacts (Vega and Rust 2001). In the Iberian Peninsula, at least two points of introduction have been detected: first observations date to 1894 in Oporto (western Iberian Peninsula), and to 1923 or possibly 1919 in Valencia (eastern Iberian Peninsula) (Espadaler and Gómez 2003). Presently, Argentine ants range along much of the coastal zone, except along the Cantabrian coast where records are scarce. Few populations are known from interior localities, except those associated with urban centers (Espadaler and Gómez 2003; Carpintero et al. 2004). Several studies have analyzed Argentine ant invasion in the region (Way et al. 1997; Espadaler and Gómez 2003; Roura-Pascual et al. 2004; Carpintero et al. 2005; Roura-Pascual et al. 2006; Carpintero and Reyes-López 2008), but none has focused on regional-scale ecological requirements of the species in this part of its introduced range.

Species' distribution patterns are eminently scale-dependent, since different ecological processes emerge depending on the spatial scale of analysis (Wiens 1989; Mackey and Lindenmayer 2001; Farina et al. 2005). Distributional patterns of Argentine ants have been studied at both large (Roura-Pascual et al. 2004; Hartley et al. 2006; Roura-Pascual et al. 2006)

and small (Hartley and Lester 2003; Krushelnycky et al. 2005) spatial scales. Here, we analyze the Argentine ant distribution at regional scales using ecological niche modeling to elucidate the main factors responsible for its present-day distribution across the Iberian Peninsula.

With the increasing use and improvement of ecological niche models in the last few decades (Guisan and Thuiller 2005; Araújo and Guisan 2006; Elith et al. 2006), it has become clear that predictions are sensitive not only to occurrence and environmental data, but also to the methods used to calibrate the models (Thuiller 2004; Pearson et al. 2006). Elith et al. (2006) have demonstrated differences in predictive performance among modeling methods, as well as significant variations among regional datasets. To deal with this variability, one solution is to develop models using multiple modeling methods and to identify consensual areas of consistent prediction (e.g., Anderson et al. (2003); Araújo et al. (2006)). Areas of consensus among predictions incorporate modeling uncertainties to produce more reliable estimates of species' potential distributions (Hartley et al. 2006). For this reason, we have developed ensemble models across modeling approaches for determining the potential distribution of Argentine ants in the Iberian Peninsula.

In addition, variations in occurrence and environmental data have long been known to produce divergences among geographic predictions. Models calibrated based on a wider range of environmental conditions are better able to outline ecological niches of species than models developed using restricted geographic areas and subsets of data, which tend to predict narrower suitable areas for the species. Hence, we also modeled potential distributions of Argentine ants based on the eastern and western sides of the Iberian Peninsula separately. The two sides present different colonization histories (Giraud et al. 2002) and ecological characteristics (Mediterranean versus Atlantic influences, respectively), which could produce divergences in invasion patterns of Argentine ants in the Iberian Peninsula. Hence, we had two objectives: (1) to determine the potential distribution of Argentine ants in the Iberian Peninsula and the environmental factors that explain the present-day occurrence of the species at regional spatial scales, and (2) to study possible divergences in the invasive process among populations within the Iberian Peninsula.

Materials and methods

The approach used herein is based on modeling species' ecological niches, here taken as the set of conditions under which a species is able to persist and maintain stable populations without immigrational subsidy (Grinnell 1917; Hutchinson 1957). Niche modeling algorithms search for non-random associations between known occurrences of the species and relevant ecological/environmental parameters in the form of digital maps; these niche models are then used to identify areas fitting the ecological requirements of the species (Soberón and Peterson 2005). A limitation, however, is when the ecological characteristics of species' present distributions do not reflect their entire ecological potential, because this ecological diversity is not fully represented on that landscape, or the species is not in equilibrium. Despite this limitation, niche models based on occurrence data from native or introduced ranges can potentially indicate some, although not all, new areas susceptible to invasion, and can elucidate ecological processes governing invasion processes (Peterson 2003).

In contrast to previous studies predicting the potential distribution of the Argentine ant in introduced areas based on occurrence data from the native area (Roura-Pascual et al. 2004; Hartley et al. 2006), we only use occurrence data from the invaded range to calibrate the models. Although Argentine ants are not known to be in equilibrium with the environment (Casellas 2004) and models might thus underestimate its potential distribution, we think that the current distribution of the species in the region provides a good estimate of its potential range based on two main facts. Firstly, we did not find significant differences in model performance between predictions derived from models calibrated using native and invaded occurrences (Roura-Pascual et al. 2006). Secondly, since the first observations were made approximately 100 years ago, the species has had time to sample a wide variety of available habitats. Based on these considerations, we preferred to use occurrence data from the invaded range to understand in great detail the main drivers of the Argentine ant invasion in the Iberian Peninsula.

Occurrence and environmental datasets

We used 350 known occurrence localities for Argentine ants across the Iberian Peninsula compiled from

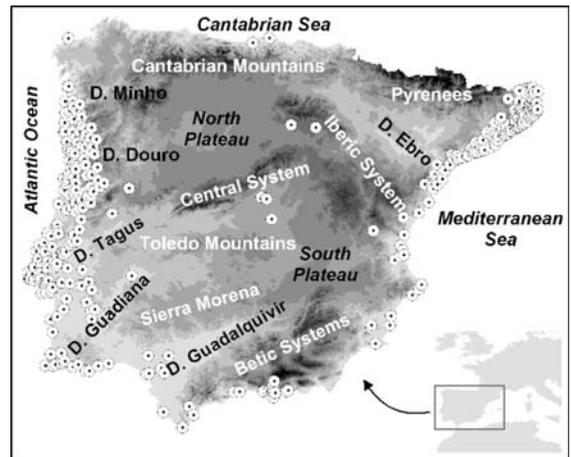


Fig. 1 Distribution of the Argentine ant in the Iberian Peninsula (SW Europe), with known occurrences indicated as dots. Darker shades indicate higher elevations

specimens at natural history museums and personal collections, scientific literature, and field surveys (full dataset provided as electronic appendices in Roura-Pascual et al. (2004)) (Fig. 1). Since absence data were unavailable, we generated pseudoabsence data for constructing the models despite being aware of their limitations (Brotons et al. 2004; Pearce and Boyce 2006).

To summarize the environmental space potentially available to Argentine ants, we used 12 coverages summarizing aspects of topography¹ (elevation (herein abbreviated as *elev*), orientation (*orient*), and slope (*slope*), derived from the 200 m resolution digital elevation model of the Iberian Peninsula, Ninyerola et al. 2005); and climate² (annual mean solar radiation (*amrad*), annual mean precipitation (*amprecip*), annual mean temperatures (*amtemp*), minimum winter mean temperatures (*minwtemp*), and maximum summer mean temperatures (*maxstemp*), from the 200 m resolution Digital Climatic Atlas of the Iberian Peninsula, Ninyerola et al. 2005); and remotely sensed data³ (16-day composites at 500 m for the Normalized Difference Vegetation Index (*NDVI*) and for the Enhanced Vegetation Index (*EVI*) from July 2005 from the NASA-MODIS/Terra

¹ <http://opengis.uab.es/wms/iberia/index.htm>

² Ibid. http://opengis.uab.es/wms/iberia/catala/ca_bibliografia.htm

³ <http://edcimswww.cr.usgs.gov>

dataset, Justice et al. 1998). These environmental data were selected according to our knowledge of the species' ecology (Holway et al. 2002; Abril 2005; Krushelnycky et al. 2005; Heller et al. 2006; Menke and Holway 2006; Menke et al. 2007; Heller et al. 2008). Minimum winter mean temperatures were obtained by calculating the mean of December, January, February, and March minimum temperatures, and maximum summer mean temperatures by calculating the mean of May, June, July, August, September, and October maximum temperatures. Months were selected according to known details of Argentine ant activity; the period May–October is when the species is most active. We also used NDVI/EVI 16-day composites from July because during this month the Argentine ant is most active (Abril 2005). All data were resampled to 600 m spatial resolution for analysis.

Ecological niche modeling techniques

Five different modeling methods were used to produce ensemble predictions. The first two methods, generalized linear models (GLM) and generalized additive models (GAM), are generalizations of classical linear regression models that have been used widely to model, explain, and predict species' distributions (Guisan et al. 2002). GLM allows for non-linearity and non-constant variance among data, whereas GAM permits non-parametric and complex relationships between the response and predictor variables, in addition to parametric forms (Hastie and Tibshirani 1990; Guisan et al. 2002). In GLM, predictor variables (i.e., the environmental data) are combined to generate linear, quadratic, and cubic parametric terms related to the expected value of the response variable (i.e., probability of presence versus absence of the species) through a logit link function (Guisan et al. 2002; Rushton et al. 2004). Although widely applied in ecological studies, GLM has difficulties in dealing with complex ecological relationships (Elith et al. 2006). By fitting non-parametric, smoothed functions of explanatory variables to the response variable without prejudging the shape of the relationship between both terms, GAM produces more flexible response curves than most classical linear models. In both GLM and GAM, the most influential variables and the required transformation (polynomial terms and degree of smoothness,

respectively) were selected through a stepwise procedure based on the AIC criterion (Akaike 1974).

We also applied a recent proposed alternative, the generalized boosted model (GBM) (Friedman 2001). Contrary to previous methods that produce single parsimonious models, GBM uses an iterative method (the boosting algorithm) for developing multiple regression trees and combining them into an ensemble prediction (Friedman and Meulman 2003). "Regression trees" are built by splitting the calibration data repeatedly, according to a simple rule based on a single explanatory variable. At each split, the data are partitioned into two exclusive groups, each of which is as homogeneous as possible. The heterogeneity of a node is defined with a deviance notion that can be interpreted as the deviance of a multinomial model (Breiman et al. 1984). Regression trees have been used successfully in ecology (Rouget et al. 2001; Thuiller et al. 2003). "Boosting" is used to overcome the inaccuracies of a single model (see discussion in (Araújo and New 2007)), and makes possible to model a complex response surface. For more details or applications in ecology, see Ridgeway (1999); Friedman (2001); Elith et al. (2006); Leathwick et al. (2006); Elith et al. (2008).

Although these three above-mentioned methods have been usually used with presence-absence data, they can be applied to presence-only situations by using pseudo-absence selected randomly from areas from which the species is not known (Brotons et al. 2004; Pearce and Boyce 2006). Herein, to calibrate final models, we generated an equal number of pseudo-absences as presence localities by selecting a random subset of pixels from the overall study area. All of these modeling techniques were run under the BIOMOD modeling application (Thuiller 2003) or R-CRAN software, which relies on the use of GLM, GAM (by T. Hastie) and GBM (by G. Ridgeway) libraries.

In contrast to this group of modeling methods, we also implemented two evolutionary-computing methods that generate pseudo-absences as an intrinsic step in the modeling algorithm, GARP and Maxent. Although they are not considered presence-only methods, these two techniques have been proved to outperform classical presence-only models assessing the distribution of species (Elith et al. 2006; Ward 2007). The Genetic Algorithm for Rule-Set

Prediction (GARP) uses different rule types (logistic regression, range rules, negated range rules, and atomic rules) to develop a rule-set defining the species' ecological niche (Stockwell and Noble 1992; Stockwell and Peters 1999), which is projected into geographic space to produce a binary map of presence versus absence. The model evolves through an iterative process of rule selection, evaluation, testing and incorporation or rejection, randomly subsetting occurrence data into training and testing data to estimate the predictive accuracy of each rule (here 50% and 50%, respectively). Then, input training presence data are resampled randomly with replacement to create a set of 1,250 presence points, and an equal number of points is also resampled randomly from the background area where the species has not been recorded (pseudoabsences). Change in predictive accuracy between iterations is used to evaluate whether particular rules should be incorporated into the model; the algorithm runs 1,000 iterations or until convergence. To optimize model performance, we developed 100 replicate GARP models and chose a "best subset" of 10 models based on error distributions for individual models (Anderson et al. 2003), which were summed to provide an estimate of potential distribution for Argentine ant.

Finally, the Maximum Entropy method (Maxent) is a machine-learning method that uses a mathematical formulation to estimate the probability distribution of a species following the principle of maximum entropy, which supposes that no unfounded constraints should be included in the estimation (Phillips et al. 2006). In constructing the probability distribution, Maxent uses different types of environmental features (linear, quadratic, product, and threshold combinations of raw continuous environmental data, as well as categorical environmental data) and a regularization parameter (β) for each feature, which estimates how close the expected value should be to the observed value (Phillips et al. 2004). For developing the model, Maxent creates random samples of background pixels (10,000) from the study area as pseudoabsences. We used the default parameters throughout. The final probability distribution developed is projected onto the geographic space, and a cumulative probability (expressed as a percentage) is assigned to each pixel, interpretable as an index of suitability for the species.

Approach for modeling Argentine ant potential distribution in the Iberian Peninsula

Our approach for comparing invasion patterns in the western and eastern Iberian Peninsula consisted of two steps. (1) We selected optimal environmental datasets for modeling the species' ecological niche, and (2) we identified the areas of consensus among modeling approaches to elucidate differences and similarities between invasion patterns of the Argentine ant within the Iberian Peninsula.

To select environmental data (Step 1), we developed 50 generalized boosted models for the overall Iberian Peninsula, and for western (UTM longitude <184,000) and eastern (UTM longitude >637,000) areas separately. First, we created three occurrence datasets: 350 localities from the whole Iberian Peninsula (herein called *Ib*), 175 localities from the western area (*wIb*), and 142 localities from the eastern area (*eIb*). Since true absence data were not available to calibrate models, an equal number of pseudoabsences were randomly resampled from each area. GBM then estimated the relative importance of each environmental variable in the model accounting for all the other variables. We used a permutation method, which randomly resamples each predictor variable independently and computes the associated reduction in predictive performance (Thuiller et al. 2006). However, to reduce uncertainties due to the random selection of pseudoabsence data, we developed 50 GBM models for each area using different subsets of pseudoabsence data. The influence of each predictor variable was computed by averaging its relative importance (following Friedman (2001)) across the 50 runs; the most relevant environmental variables in each area were retained, and three separate environmental data-subsets thus obtained to develop final models of Argentine ant distribution. The GBM approach averages the relative influence of each variable across all trees generated by the boosting algorithm, giving a relatively robust and stable estimate (Friedman 2001); we did not use the other approaches to estimate the relative importance of variables because we believe that this boosting approach is the most reliable and unbiased, and because comparing the choice of variables among models was not the point of the paper.

Finally (step 2), using the environmental data selected, we developed ensembles of models for

overall, western, and eastern portions of the Iberian Peninsula. First, we divided occurrence data randomly (including presence data and an equal number of pseudoabsences) from each area into training (70%) and testing (30%) datasets for calibrating and testing the accuracy of models, respectively. With the training data and the previously selected environmental data, we developed models for the entire, as well as the eastern and western Iberian Peninsula areas, using GLM, GAM, GBM, GARP, and Maxent. Model performance was tested using the independent testing data set aside from model development. To reduce uncertainty caused by sampling artifacts (generated during the random resampling of presence localities and generation of pseudoabsence), we calibrated 10 replicate models for each area and modeling technique by using different combinations of training data. While presence data were selected randomly from the initial pool of Argentine ant localities, pseudoabsences were resampled each time, selecting points from the area without confirmed presence of the species.

Each set of 10 replicate models was finally transformed into a single model via a weighted model average (Eq. 1). Model weights were assigned so as to enhance contributions of those models with higher model performance values (measured by the *AUC* of a ROC analysis) relative to the set of plausible models developed using the same modeling technique and calibration area, but based on different subsets of occurrence data, allowing us to discern differences among modeling approaches.

$$g_M(X) = \sum_{m=1}^{10} \omega_m \cdot p_m(X) \quad \text{where} \quad \omega_m = \frac{AUC_m}{\sum_{m=1}^{10} AUC_m} \quad (1)$$

where $p_m(x)$ is the value predicted by each replicate model (m), developed applying one of the five modeling approaches and different training data-subsets; ω_m is the weight assigned to each replicate model taking into account its model performance, measured using the area under the curve (AUC_m), in relation to the mean model performance of the overall set of replicate models.

However, given our interest in identifying patterns of consensus among predictions of Argentine ant distribution from different modeling techniques, we also averaged final model predictions obtained by

each modeling approach. As previously showed (Eq. 1), we assigned weights depending on comparisons with the average *AUC* of the set of replicate models for each modeling approach (see Eq. 2). This approach allowed us to identify consensus areas for Argentine ant potential distribution.

$$c(X) = \sum_{M=1}^5 \omega_M \cdot g_M(X) \quad \text{where} \quad \omega_M = \frac{AUC_M}{\sum_{M=1}^5 AUC_M} \quad (2)$$

where $g_M(x)$ is the weighted average value for each modeling approach (M) obtained using Eq. 1, and ω_M is the weight assigned to each averaged prediction taking into account model performance, measured as the mean area under the curve (AUC_M) of the ten individual models developed using that particular modeling approach (Eq. 2). Finally, to identify and localize discrepancies among modeling methods in predicting potential distributions of the Argentine ant, we measured the variance among averaged predictions, which gave us greater confidence in our final results and permitted us to represent geographically uncertainties among methods (Hartley et al. 2006).

Throughout, model performance was tested using the Receiver Operating Characteristic (ROC) analysis (Hanley and McNeil 1982) implemented in R-CRAN software (function ‘*somers*’ from the ‘*Hmisc*’ library). ROC analysis evaluates model performance independently of arbitrary thresholds for presence, and has been used extensively in distribution modeling studies owing to its nonparametric threshold-independent nature (Manel et al. 2001). Overall model performance is summarized as the area under the curve (*AUC*), interpretable as the probability that a model discriminates correctly between presence and absence sites (Pearce and Ferrier 2000). *AUC* values range 0–1, where $AUC = 1$ indicates perfect model performance, and $AUC = 0.5$ indicates predictive discrimination no better than random.

Additional statistical analyses

We used a repeated-measures ANOVA to assess how model performance (measured by means of *AUC* values) varied between modeling approaches (five levels: GLM, GAM, GBM, GARP, Maxent) and areas of calibration (three levels: *lb*, *elb*, and *wlb*), respectively. We considered modeling approaches

and areas of calibration as fixed factors, and occurrence data-subsets used for training and testing the replicate models in each area (ten levels par area of calibration: number of iterations performed in step 2) as random factors. Repeated-measures ANOVA permitted us to deal with the non-independence in the model performance measures between predictions calibrated using the same occurrence dataset. The analysis was performed using the *lme* function, which performs mixed linear models, implemented in R-CRAN.

To investigate environmental relationships between eastern and western occurrence localities, we followed the methodology of Broennimann et al. (2007). A PCA analysis was conducted to visualize (in a bivariate plot of the two main factors of a PCA) variation patterns among occurrences for western and eastern areas. To search for environmental similarities/dissimilarities among ecological niches on both sides of the Iberian Peninsula, after performing a PCA analysis for eastern and western localities separately, factor coordinates of the first two principal components of each PCA were compared.

Results

Selection of environmental data

After performing a first correlation analysis, we eliminated *minwtemp* and *EVI* from the modeling exercise owing to their high correlation ($r > 0.8$) with other environmental variables. *Minwtemp* was highly correlated with *elev* and *amtemp*, and *EVI* was only correlated with *NDVI*, which is more chlorophyll-sensitive and can have a greater influence on Argentine ant distribution than *EVI* (Huete et al. 2002).

The averaged results of the 50 replicate GBM models identified the most relevant environmental variables, i.e. those with high values of relative influence, for predicting Argentine ant distributions in each area (Fig. 2). For Iberian-based models, the most relevant environmental variables were *elev*, *amtemp*, *maxstemp*, *amprecip*, and *slope*. Somewhat different results appeared when using eastern and western localities only: while western-based models also indicated *NDVI* as relevant, eastern-based models identified only *elev*, *amtemp*, and *amprecip* as relevant.

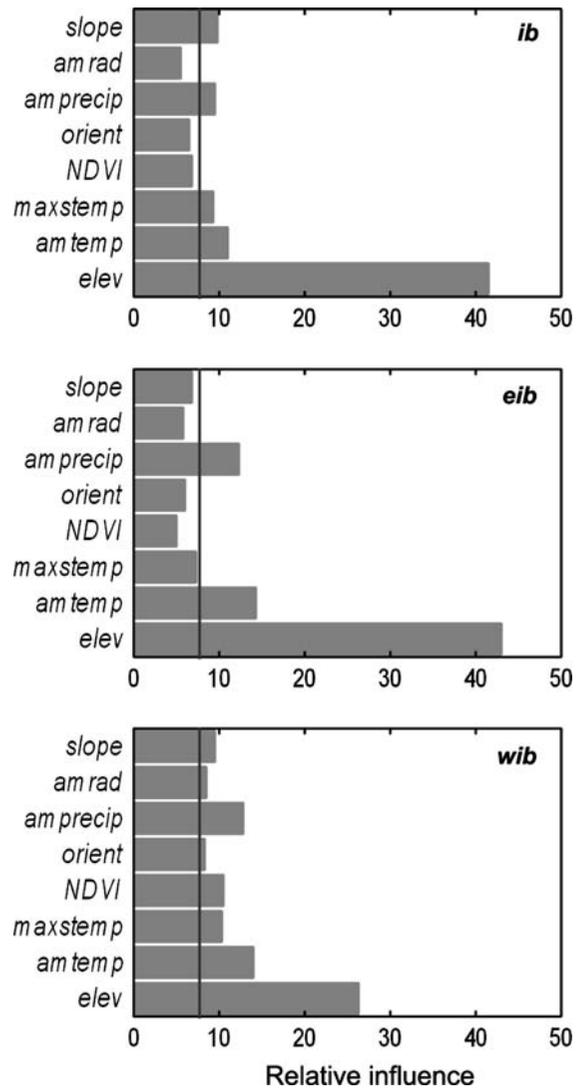


Fig. 2 Most relevant environmental variables in predicting Argentine ant distributions in areas of the overall (*ib*), eastern (*eib*), and western Iberian Peninsula (*wib*) using generalized boosted models (step 1). Bar refers to mean relative influence of each variable developed applying the same environmental dataset to 50 different subsets of occurrences. For visualization, the dotted line indicates the threshold (relative influences = 8) used to include or exclude particular variables from further analysis

Comparison between niche predictions

For modeling Argentine ant distribution across the entire peninsula, and in the eastern and western sectors separately, we developed 10-replicate models by combining the most influential variables for each region with 10 different subsets of training occurrence

data from each area. These sets of replicate models were calibrated using different modeling techniques to reduce divergences among methods and produce ensemble predictions. The weighted average of *AUC* values of each set of 10-replicate models ranged between 0.77 and 0.95 (mean *AUC* = 0.87; Fig. 3), which indicated overall good ability to predict the distribution of the species. However, variation in predictive performance between modeling approaches was statistically significant (Table 1). Highest values of model performance were attained by Maxent models, and lowest by GARP models.

Despite these differences, all modeling methods showed similar trends in predicting Argentine ant

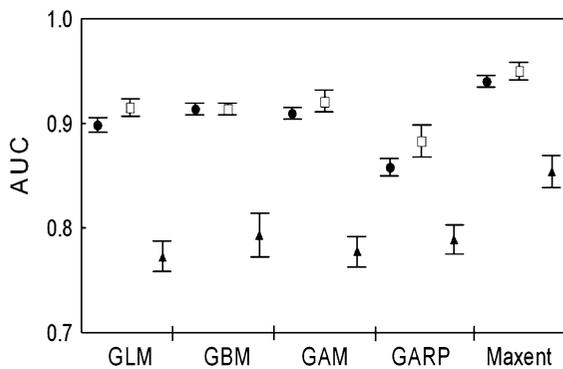


Fig. 3 Differences in model performance between modeling approaches depending on the area used for calibrating the models: overall Iberian peninsula (represented by ●), eastern Iberian Peninsula (□), western Iberian Peninsula (▲). The y-axis presents the mean *AUC* value of each set of predictions developed applying the same environmental dataset to different subsets of occurrences. Whiskers show standard errors

Table 1 Repeated-measures ANOVA assessing changes in model performance between modeling approaches and areas of calibration

| Source of variation | Model performance (<i>AUC</i>) | | | |
|----------------------|----------------------------------|--------|-----------------|-----------------|
| | Num df | Den df | <i>F</i> -value | <i>P</i> -value |
| Intercept | 1 | 116 | 23458.145 | <0.0001 |
| Modeling approaches | 4 | 116 | 28.780 | <0.0001 |
| Areas of calibration | 2 | 27 | 44.232 | <0.0001 |

The analysis was performed using linear mixed effects models. Modeling approaches (five levels: GLM, GAM, GBM, GARP, Maxent) and areas of calibration (three levels: *lb*, *elb*, and *wlb*) were included as fixed factors, and occurrence data-subsets used for training and testing the replicate models in each area (ten levels par area of calibration: number of iterations performed in step 2) as random factors

distribution (Fig. 3). Models developed using occurrence data from the entire Iberian Peninsula gave *AUC* values between 0.86 and 0.94 (mean *AUC* = 0.90). Whereas eastern-based models gave similar *AUC* values of 0.89–0.95 (mean *AUC* = 0.92), western-based models produced lower *AUC* values (ranging 0.77–0.85, mean *AUC* = 0.80). This observation was corroborated by the repeated-measures ANOVA, which found significant differences in predictive performance depending on the area: western-based models presented lower model performance than eastern or overall-based models (Table 1).

Visual comparisons of model predictions also revealed some divergences: GARP predicted the largest area suitable for Argentine ants and Maxent the narrowest areas at the highest predicted thresholds, whereas GLM, GAM, and GBM presented intermediate predicted areas (Fig. 4). However, ensemble predictions for the overall, eastern and western areas coincided in indicating coastal areas and river valleys as highly suitable for Argentine ants (Fig. 5). Nevertheless, taking into account the variability among final predictions, some areas (e.g., most river courses, and northern and southeastern coastal areas) presented high levels of variance among models.

Restricted to the initial non-correlated environmental variables, the principal component analysis aimed to describe the relationship between eastern and western localities of the Argentine ant. The first two axes of the PCA accounted for 41% of total variance: PC1 (26% of variance) was positively correlated with *NDVI* ($r = 0.53$) and *amprecip* ($r = 0.49$), and negatively correlated with *amtemp* ($r = -0.33$); PC2 (15% variation) was negatively correlated with *maxstemp* ($r = -0.58$) and *orient* ($r = -0.47$; Fig. 6). Comparisons of environmental conditions between western and eastern localities indicated some similarities, and some divergences: while occurrence data on the two sides of the Iberian Peninsula presented similar precipitation gradients, western localities seemed to occupy a larger radiation range (i.e., lower values of *maxstemp* and *orient*) than eastern localities. This pattern was confirmed by developing additional principal components analyses for each side of the Iberian Peninsula. The first factors (PC1) of each analysis were significantly correlated between areas ($r = 0.95$), but the second factors (PC2) presented a low correlation ($r = 0.15$). This result thus indicated that occurrence data of the

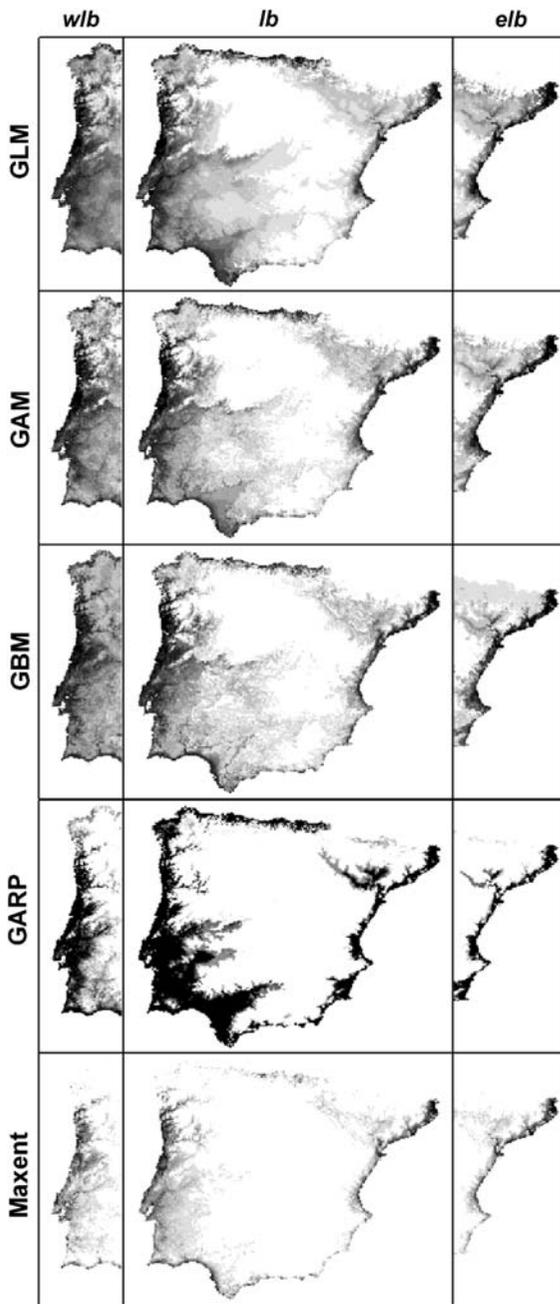


Fig. 4 Predicted potential distribution of Argentine ant in the Iberian Peninsula using different modeling approaches. Columns indicate the calibration area of the models, while rows indicate the modeling approach used: GLM, GAM, GBM, GARP, and Maxent. Note that models developed for each area were calibrated using different environmental datasets (see Results). Higher probabilities in predicting the potential geographic distribution of the Argentine ant are indicated in darker shades

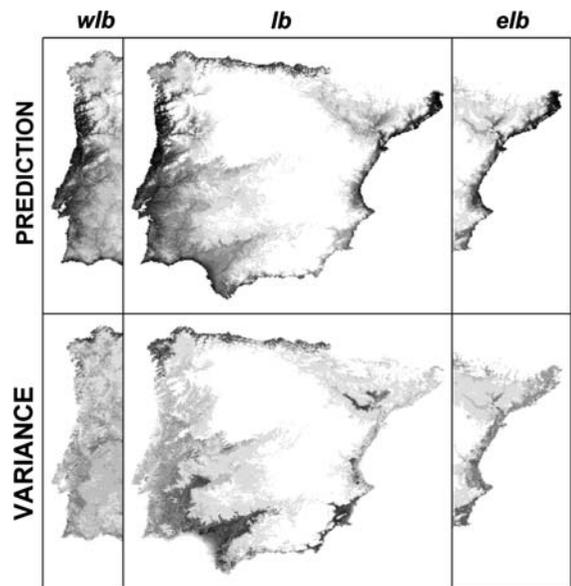


Fig. 5 Areas of consensus and variance among modeling approaches in predicting Argentine ant distribution in the Iberian Peninsula. The first row shows areas of consensus among predictions developed using GLM, GAM, GBM, GARP, and Maxent, while the second row shows the variance among them. Darker shades indicate higher agreement (first row) and higher variance (second row) between modeling approaches in predicting the potential geographic distribution of the Argentine ant

species at both sides of the Iberian Peninsula, although highly similar, are influenced in different ways by environmental conditions.

Discussion

In this exercise, we identified the most influential variables in determining Argentine ant distribution using generalized boosted models (GBM). In general, the species' distribution appears highly dependent on the shape of the elevation gradient over the entire Iberian Peninsula. However, other climatic variables (annual mean temperature and annual mean precipitation) were also important in refining our predictions. This result is consistent with our knowledge of the species, which is not known to occur in cold and dry areas of the Iberian Peninsula (Espadaler and Gómez 2003), and also with the spatial resolution of our analyses, which does not allow us to consider smaller-scale processes that restrict the species' distribution

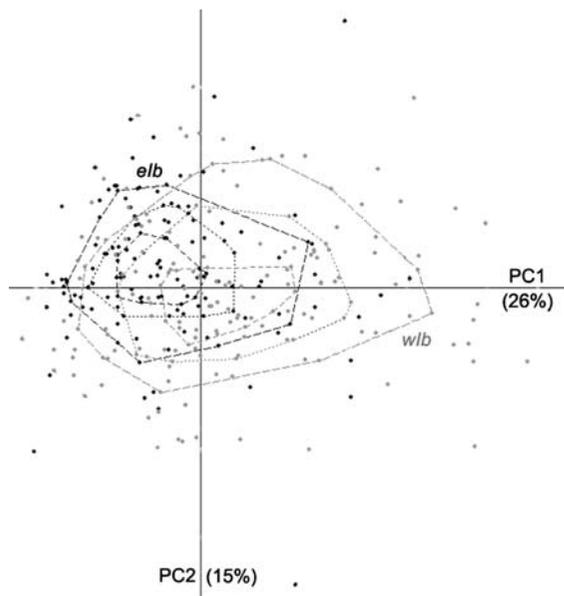


Fig. 6 Visualizations of environmental conditions of Argentine ant occurrence localities in the Iberian Peninsula in a bivariate plot of two principal components, which summarize variation among the environmental variables included in the modeling exercise. Black dots refer to occurrence data from the eastern side, while grey to western occurrences. Different lines represent the convex hulls, including 25%, 50% and 75% of the overall occurrences for each area

locally, such as anthropogenic disturbances or presence of watercourses (Carpintero et al. 2004; Menke and Holway 2006; Menke et al. 2007).

It is also important to notice that elevation has a stronger influence in the east than in the west, where other variables (maximum summer mean temperature, NDVI vegetation index) seem to be more influential on the species' distribution. We suspect that altitude has a lower influence in western-based models because topography is more homogeneous in the west, and it does not seem to constrain Argentine ants as much as on the eastern side, where elevations are higher. Moreover, because of Atlantic influences (lower temperatures, higher precipitation), Argentine ant distribution on the western side of the Iberian Peninsula would be more constrained by maximum summer temperature and vegetation-related variables than eastern localities. This result is supported by Way et al. (1997), who suggested that the species' distribution on the western side is constrained principally by soil type and vegetation. Contrarily, Mediterranean influences (with less precipitation and higher mean temperatures) on the eastern side restrict

Argentine ants to low elevations near the coast with temperate climates (characterized by cool temperatures and higher levels of humidity). Holway (1998) suggested that Argentine ant distribution in Mediterranean California is highly dependent on moisture levels. In dry environments, Argentine ant populations seem to be highly limited by proximity to permanent watercourses and rainfall patterns (Human et al. 1998; Menke et al. 2007; Heller et al. 2008).

Differences between the eastern and western sides of the Iberian Peninsula were expected, since models were calibrated in different areas (Van Horne 2002; Thuiller et al. 2004; Pearson et al. 2006). However, it is essential to determine whether these differences result simply from environmental differences between areas or from real ecological divergences between the two populations of Argentine ants (Roura-Pascual et al. 2006). A better knowledge of overall factors influencing the Argentine ant distribution within the Iberian Peninsula would permit to refine our predictions and establish more reliable guidelines in future management practices.

Indeed, the accuracy of our niche models in predicting Argentine ant distributions is highly dependent on the occurrence data and environmental coverages included in the analysis (Stockwell and Peterson 2002). Based on our previous experience with the same occurrence dataset, we consider the >100 occurrence localities to have been sufficient to predict Argentine ant distributions (Roura-Pascual et al. 2006). Moreover, the best model performance was attained using 3–6 predictor variables, which seem to be an adequate number (Peterson and Cohoon 1999). However, because these variables have been selected using only GBM, some biases enhancing the performance of this modeling approach in front of the others might have been introduced. Nevertheless, the suitability of both occurrence and environmental data seems corroborated by the high values of model performance ($AUC > 0.7$) attained in our final predictions (Fig. 3).

However, we also found slight differences between predictions depending on the method used to calibrate the model. While Maxent showed the highest model agreement between localities of Argentine ants and model predictions, GARP performed more poorly than all other methods, and GLM, GAM and GBM presented intermediate values of model performance. These results coincide generally with results of other

comparative studies (Elith et al. 2006). However, Peterson et al. (2008) evidenced that these results are extremely biased by the evaluation technique, which favours algorithms that predict across the whole range of predicted thresholds (such as Maxent) in detriment of those models that make only predictions at the end of the spectrum (such as GARP). From a geographic point of view, these results in the model performance's value are consistent with the fact that GARP predicted broader areas as highly suitable for the species than the other methods, whereas Maxent tended to distinguished maximally among presence and absence test data and fit predictions more closely to the known distribution of the species at higher predicted thresholds. These divergences among modeling techniques, and the lack of a standardized criterion to select the most reliable prediction, suggest that conclusions based on areas of consensus can be more reliable than those derived from individual models developed via a single modeling approach. In addition, the use of consensual predictions allows identifying areas of disagreement between modeling approaches. More than simple artifacts, these discrepancies indicate regions where the invasive potential of the species is not well understood, and where studies should be conducted to refine our knowledge of the biological invasion (Hartley et al. 2006). However, further refinements of the process (principally in relation to the environmental data selection, and the implementation of the weighting scheme) should be developed to produce an objective framework in which to conduct consensual modeling approaches. The advantage of using consensual models is that they incorporate most of the uncertainties into the picture (Thuiller 2004; Araújo and New 2007). This is especially important in this study, where models calibrated using only records from the invaded range might underestimate the potential range of the species (Welk 2004).

Given the current distribution of the Argentine ant, predictions of its potential ensemble distribution across the Iberian Peninsula suggest that a further expansion of the species is possible along the coast and into inland areas along river valleys. Mountain ranges and inland plateau are predicted as highly unsuitable for Argentine ants. Since river courses make it easy for the species to enter far inland, scrutiny efforts should focus along the Ebro, Guadalquivir, Guadiana, Tagus, Douro, and Minho river valleys to look after future expansions into the

interior of the Iberian Peninsula. Moreover, although northern and southeastern coasts also appear suitable for the Argentine ant, further research is necessary to determine the species' real distribution in these areas where model predictions are variable. Expansion of the invasion along the Cantabrian coast is probably limited by lower temperatures, but on the Betic Systems coast by higher temperatures and extreme drier conditions. Special attention should also be paid at some interior areas of the Guadiana, Guadalquivir and Ebro depressions, where variance among model predictions is high. In these interior areas, *L. humile* will probably be limited to moist areas or along watercourses (Holway 1995; Human et al. 1998).

Nevertheless, to size up whether herein developed models are underestimating the species' potential distribution or not, we compared our predictions (Fig. 5) with those predictions obtained in Roura-Pascual et al. (2006) using occurrences from both native and invaded ranges to determine the ecological niche of the Argentine ant in the Iberian Peninsula. Both studies used the same set of occurrence data from the invaded range and similar spatial scales, but slightly different environmental data and modeling approaches. In general, invaded-based predictions from both studies indicate coastal areas and major rivers as highly suitable for the species. However, when compared with native-based models in Roura-Pascual et al. (2006), predictions developed in this study might underestimate the suitability of inland plateaus for Argentine ants and overestimate the capacity of the species to occupy northern coastal areas. In fact, the Cantabrian Coast was already identified as a highly uncertain region by ensemble predictions (Fig. 5). Contrarily, although potential ensemble distributions were also highly variable in river valley depressions, native-based models seem to corroborate the vulnerability of these areas to become invaded by the Argentine ant. Especially important are the Guadalquivir and Ebro depressions, where native-based models predict high values of suitable for the species.

Additionally, comparing ensemble predictions for western and eastern areas derived from models calibrated using occurrences from each area separately with predictions calibrated using occurrences from the overall Iberian Peninsula (i.e. using a wider range of environmental characteristics), differences are small. As in other studies (Peterson et al. 1999),

these results indicate that Argentine ant populations on the two sides of the Iberian Peninsula occupy similar ecological conditions and, therefore, present similar ecological niches. This idea is corroborated by the PCA analyses, which indicate that environmental characteristics of Argentine ant localities at western and eastern Iberian Peninsula are correlated.

The small divergences observed between predictions could be simply sampling artifacts or may reflect slight differences in the species' ecological niche (Broennimann et al. 2007). Real ecological niche differences between western and eastern populations, not due to modeling artifacts (Roura-Pascual et al. 2006), could result from different origins of introduced populations, as the existence of two supercolonies of the Argentine ant seems to indicate (Giraud et al. 2002). The eastern supercolony (so-called Catalan colony) is differentiated from the main supercolony that is spread more broadly in the Peninsula (Giraud et al. 2002). However, since the first reference to Argentine ant occurrence in the Iberian Peninsula was earlier on the western side (1894 in Oporto) than on the eastern side (1923 in Valencia, probably 1919; Espadaler and Gómez 2003), and the so-called Catalan colony is restricted to the northeastern side of the Iberian Peninsula, we cannot conclude with certainty that these slight divergences reflect real ecological niche differences. Contrarily, these divergences may be the results of the invasion history and/or environmental differences between both sides of the Iberian Peninsula (Roura-Pascual et al. 2006).

Conclusions

This modeling exercise attempts to understand factors responsible for shaping Argentine ant distributions in the Iberian Peninsula, and to identify the areas most vulnerable to be invaded by the species. However, given its anthropophilic tendency and opportunistic requirements for propagule pressure (Hee et al. 2000), Argentine ant expansion is expected to occur mostly in populated areas (especially coastal areas and river valleys) of the Iberian Peninsula, where opportunities to control invasions effectively are few. In this sense, although screening areas suitable for the species cannot provide a basis for establishing preventive guidelines for the overall Peninsula, it can help to plan local measures in areas where Argentine ants cause

problems to humans (e.g., building infestations) or natural ecosystems (e.g., threaten biodiversity or ecosystem functioning; Passera 1994).

In this sense, our results indicate that Argentine ants still have potential for further expansions in the Iberian Peninsula, especially along coastal areas and water-courses. Argentine ant distributions seem to be influenced principally by altitude, mean temperature, and precipitation. However, future studies should aim to characterize the suitable range for the species at local scales. Special attention should be focus on areas of maximum uncertainty among models, to elucidate the ultimate drivers of the species' distribution. On the other hand, although our results suggest that different populations of Argentine ant within the Iberian Peninsula present similar ecological niches, more specific studies of ecological divergences of populations are necessary to improve niche predictions and identify areas environmentally resistant to invasion.

Finally, from the methodological point of view, use of ensemble predictions to identify the potential distributional areas of invasive species provided new insights into the development of an objective framework on consensus modeling. Future studies of methods for selecting environmental data and selecting weighting schemes would permit more objective, consensus-based predictions.

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