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NICHE DIFFERENTIATION AND FINE-SCALE PROJECTIONS FOR ARGENTINE ANTS BASED ON REMOTELY SENSED DATA

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Abstract. Modeling ecological niches of species is a promising approach for predicting the geographic potential of invasive species in new environments. Argentine ants (*Linepithema humile*) rank among the most successful invasive species: native to South America, they have invaded broad areas worldwide. Despite their widespread success, little is known about what makes an area susceptible—or not—to invasion. Here, we use a genetic algorithm approach to ecological niche modeling based on high-resolution remote-sensing data to examine the roles of niche similarity and difference in predicting invasions by this species. Our comparisons support a picture of general conservatism of the species' ecological characteristics, in spite of distinct geographic and community contexts.

Key words: biological invasions; ecological differentiation; ecological niche; Genetic Algorithm for Rule-set Prediction (GARP); Iberian Peninsula; invasive spread; Japan; Linepithema humile; *moderate resolution imaging spectroradiometer (MODIS); North America; remote sensing; South America.*

Introduction

Biological invasions are a significant consequence of, and component of, human-caused global change (Vitousek et al. 1997). Although biotic invasions are neither new nor an exclusively anthropogenic phenomenon, the number and extent of nonnative species is increasing at a rapid rate as a consequence of increased human mobility (Levine and D'Antonio 2003, Drake and Lodge 2004). These human-caused invasions alter global environments, generating important environmental, societal, and economic impacts (Mack et al. 2000); indeed, consequences of these changes are so important that new tools are needed to facilitate prevention of invasions and control of nonnative species. By this token, approaches for modeling geographic distributions of species have seen increasing application in recent years (Guisan and Zimmermann 2000), and their extension to species' invasions (Peterson 2003, Thuiller et al. 2005) represents promising new possibilities.

The Argentine ant (*Linepithema humile*; see Plate 1) is one of the five ant species ranking among the world's 100 worst invaders, according to the web site of the Invasive Species Specialist Group of the World Conservation Union.[9] Native to northern Argentina, southern Brazil, Uruguay, and Paraguay (Tsutsui et al. 2001, Wild 2004), it is now established in many parts of the world owing to human-mediated transport (Suarez et al. 2001, Roura-Pascual et al. 2004). Introduced populations of this species can cause severe ecological and economic effects (Holway et al. 2002*a*).

As with most invasive species, multiple factors contribute to the success of Argentine ant populations in introduced ranges. For example, Argentine ants have been introduced without their coevolved natural enemies, and the ant communities they invade tend to be depauperate relative to the species-rich ant fauna of southern South America (Suarez et al. 1999, Holway et al. 2002*a*, Heller 2004). Moreover, Argentine ants appear to be better competitors than the native species they generally displace (Human and Gordon 1997, Holway 1999). Recent studies suggest that phenotypic and genetic changes occurring during or after introductions may influence invasive success (Ross et al. 1996, Tsutsui et al. 2000, Holway and Suarez 2004). While these studies focus primarily on behavioral differences or changes in colony structure, changes in physiology or

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PLATE. 1. Argentine ant (*Linepithema humile*) tending scale insects on citrus trees in California, USA. Photo credit: A. L. Wild.

tolerance to environmental conditions could also affect the extent to which invasive species can invade new environments. The consequences of these changes for the success of Argentine ants in invading new environments remain unknown; clearly, further detailed comparisons between native and introduced populations are necessary.

In this study, we examine differences in ecological niche characteristics of Argentine ants between native and introduced populations to understand ecological changes that may or may not have occurred and to predict the potential for future invasions. Species' geographic distributions are influenced by their ecological niches, the set of environmental conditions within which a species can maintain populations without immigrational subsidy (Grinnell 1917). Although several studies (Huntley et al. 1989, Peterson et al. 1999, Martínez-Meyer et al. 2004) have observed general conservatism in species' ecological niches on evolutionary time scales, few studies have assessed the stability of niche characteristics when populations are transplanted to another continent presenting a distinct biotic community context (Fitzpatrick and Weltzin 2005). Introduced species tend to establish populations in areas matching the environmental conditions of their native distributional areas (niche stability or niche conservatism) (Peterson 2003). Nonetheless, it is possible that shifting interactions given biotic community differences between distributional areas or evolutionary changes post-introduction may produce shifts in ecological niche characteristics (niche differentiation/evolution) (Peterson and Holt 2003, Wiens and Graham 2005).

We build on our previous studies of potential geographic distributions of *Linepithema humile* at global scales for present and future climate scenarios (Roura-Pascual et al. 2004), as well as on work at local scales by Hartley and Lester (2003), by comparing native and invaded-range ecological niches of this species at high resolution. Our approach permits analysis of ecological requirements for successful invasion by Argentine ants at regional scales, providing an opportunity to test whether differences in invasion success across introduced populations correlate with recent evolutionary changes. Finally, this study tests the utility of remote-sensing data for predicting the geographic potential of invasive species.

METHODS

A tested approach for estimating species' ecological niches is the Genetic Algorithm for Rule-set Prediction (GARP; Stockwell and Peters 1999, Anderson et al. 2003, Peterson 2003). The GARP is an evolutionary-computing approach that searches for nonrandom associations between occurrences of species (georeferenced localities in geographic coordinates) and environmental variables (i.e., digital maps of relevant ecological parameters). Inspired by models of genetic evolution, GARP models are composed of sets of rules that were "evolved" through iterative processes of rule selection, evaluation, testing, and incorporation or rejection.

Input data

Georeferenced localities on which we based our models were extracted from museum specimen locality records and personal collections, scientific literature, and field surveys (for the full set of localities see the appendix in Roura-Pascual et al. [2004]). Overall, we used 64 occurrence points from the native distributional area, and 341, 280, and 9 points from invaded areas in the Iberian Peninsula, North America, and Japan, respectively.

The environmental data sets included 30 digital maps ("coverages") summarizing aspects of topography (elevation, topographic index, slope, aspect, flow direction and flow accumulation, from the U.S. Geological Survey's Hydro-1K data set [*available online*],[10] spatial resolution 1 × 1 km) and 16-day composite remotely sensed data layers (one composite per month during 2003 of the Normalized Difference Vegetation Index [NDVI] and the Enhanced Vegetation Index [EVI] from the spaceborne NASA-MODIS/Terra optical imager [*available online*][11] at a spatial resolution of 500 × 500 m; Justice et al. [1998]). Differences in summer/winter timing between Northern and Southern Hemispheres were resolved by shifting Southern Hemisphere monthly data by six months and thus aligning northern and austral summers and winters appropriately. The two vegetation indices are derived reflectance values measured in the visible and near-infrared domains and are complementary; while NDVI is more sensitive to chlorophyll content, EVI ($L = 1$; $C1 = 6$; and $C2 = 7.5$ as equation coefficients) is more responsive to canopy structural variations (Huete et al. 2002). Thus, these indices act as surrogates for land cover variables and as such are closely related to climatic dynamics (Egbert et al. 2002). Climatic data were not taken into account directly because of the lack of such data at appropriately fine resolution for all areas. All geographic data were resampled to 1 km resolution to facilitate analysis across broad spatial extents.

The GARP algorithm

The GARP maps occurrence data into a regular grid at the same scale and extent as the environmental data, allowing only one occurrence to be selected from each pixel. First, grid cells holding known occurrences are divided into data input into the genetic algorithm for model development and an independent data set ("extrinsic testing data") for evaluation of model quality at user-specified proportions (here, 50% and 50%, respectively). Then the input data are resampled with replacement to create a set of 1250 presence points; an equal number of points is also resampled randomly from the set of grid pixels at which the species has not been recorded (pseudo-absences). The input data are further subdivided into training data (for rule development) and intrinsic testing data (for evaluation of rule predictivity). Changes in predictive accuracy from one iteration to the next are used to evaluate whether particular rules should be incorporated into the model or not, and the algorithm runs either 1000 iterations or until convergence. The final ecological niche model rule-set is then projected onto the digital maps that are the environmental data set's input into the algorithm to identify areas fitting the model parameters, a hypothesis of the potential geographic distribution of the species.

Subsequently, once the final rule-set (or individual model) is developed, predictive accuracy of each model is also evaluated based on the extrinsic testing data. Spatial predictions of presence and absence can hold two types of error: omission (areas of known presence predicted absent) and commission (areas of known absence predicted present), which can be summarized in a measure of predictive accuracy as the percentage of points correctly predicted as present or absent (the correct classification rate of Fielding and Bell [1997]).

Given the stochastic nature of GARP (both via sampling of occurrence data and the genetic algorithm itself), it produces distinct results for alternate runs based on the same input data, representing alternative solutions to the computational challenge. Following recently proposed best-practices approaches (Anderson et al. 2003), we developed 100 replicates of each model (previous tests with 1000 replicates showed that more models do not improve the final best-subset models, but do meet with computational limitations); of these, we retained the 20 models with lowest omission error and then discarded the 10 models of these 20 that presented the most extreme values of area predicted present (the "commission error index" of Anderson et al. [2003]). These "best-subset" models were summed to produce final predictions of potential distributions.

Models were validated using the receiver operating characteristic (ROC) analysis, which evaluates model performance independently of arbitrary thresholds at which presence might be accepted (Fielding and Bell 1997, Manel et al. 2001, Pearce and Boyce 2006). The ROC analysis assesses model performance by plotting sensitivity (proportion of presence points correctly predicted) vs. 1 − specificity (proportion of absences correctly predicted) across all possible thresholds. Because true absences were not available for all areas, pseudo-absences (any pixel without confirmed presence) were employed as surrogates (Wiley et al. 2003, McNyset 2005). Given computer limitations, the ROC analysis was performed on a randomly selected subset (5%) of the overall predicted areas. Good model performance is characterized by large areas under this curve (AUC; maximizing sensitivity for low values of 1 − specificity): AUC values of 0.5 indicate models with no accuracy, while AUC values of 1.0 indicate high accuracy. A z statistic was used to compare observed AUC with the random AUC (following formulas in Hanley and McNeil [1982]) or between AUCs for two independent analyses (following formulas in Hanley and McNeil [1983]); if $z > 1.96$, then the probability is <0.05

[10] ⟨http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html⟩

[11] ⟨http://edcimswww.cr.usgs.gov/pub/imswelcome/⟩

that the observed difference would be expected at random.

Modeling approach of this study

The overall approach used to compare ecological niches of Argentine ants in different regions (native distribution, Iberian Peninsula, North America, and Japan) consisted of three steps. Step 1 was designed to optimize the environmental data sets for predicting the species' ecological niche in succeeding steps. Hence, we used a cross-validation analysis between two regions: models based on occurrences from the native range were projected onto the Iberian Peninsula and vice versa, and model performance was tested using ROC on the projected region using the occurrence data set aside from model development. Seven predictions were developed for each occurrence data set, representing all combinations of suites of environmental data sets: topography (H), NDVI (N), and EVI (E) combined for analysis as H, N, E, HN, HE, NE, and HNE. Based on results of these cross-validation analyses, taking higher test AUC scores as an indication of a better environmental data set for characterizing that species' ecological niche, we chose a suite of environmental data sets for further analyses.

In step 2, we tested the suitability of each occurrence data set within each region when possible, given sample sizes (i.e., excluding Japan). Occurrence data were divided into two subsets for training and testing model performance in geographically separate areas, as follows. Native-range occurrences were divided depending on their location on a 2° × 2° checkerboard (44 occurrences for set 1 and 23 occurrences for set 2); Iberian Peninsula were divided into eastern (<2° W longitude, 206 occurrences) and western (>6° W longitude, 176 occurrences); and North American occurrences were divided into eastern (<100° W longitude, 123 occurrences) and western (>108° W longitude, 156 occurrences). We validated within-region model predictivity using one of the subsets listed above to predict the other, and vice versa, and evaluated model performance using ROC. As this test forces the model to predict areas from which no occurrence points were used in training the model, high AUC values indicate the ability of models to predict broadly unsampled regions.

In step 3, we performed an overall cross-prediction analysis, building models and predicting between all regions to assess the strength of niche differences. Each regional occurrence data set (native range, Iberian Peninsula, North America, Japan) was modeled using GARP, and the resulting ecological niche model (ENM) was projected onto every other regional data set. The ENM performance in predicting "other" regions was evaluated using the ROC procedure described above. High AUC values indicate that model predictions are better than random expectations, i.e., how well the model generated in one region correctly predicted the occurrence data of another region; because the ROC approach simply concludes that a prediction is (or is not) better than random, we also present basic statistics on model performance (i.e., omission, commission).

To visualize ecological niche differences between different models developed, we used principal components analysis to reduce the 30 initial input variables to the first two principal components, which explained the bulk of variance in ecological space. Given limitations on computer memory, we subsampled grids randomly at a density of 1:500 and used this reduced suite of grid squares for visualizations, in which we related areas of modeled presence to overall availability of environmental conditions.

Results

Selecting environmental data sets

The ROC tests performed on projections from the native-based models to the Iberian Peninsula region and vice versa yielded significant z values ($P < 0.001$) for all combinations of environmental data sets (H, N, E, NE, HN, HE, and HNE), indicating substantial capacity for all environmental data sets in predicting the species' distribution. Projections from the native-based model to the Iberian Peninsula presented AUCs ranging from 0.53 for E alone to 0.76 for HE. Still high values of AUC, indicating useful predictions, were obtained based on all environmental variables (0.73 for HNE) or with topography alone (0.75 for H). Similarly, projections from the Iberian Peninsula to the native range gives AUCs between 0.59 (H) and 0.71 (N). Although the somewhat lower AUCs suggest lower accuracy than native-range models, all models appear capable of predicting the species' range. Overall, according to the ROC tests and visual comparisons among native-range and Iberian Peninsula predictions (not shown), our interpretation is that the combination of topographic information with both vegetation indices (HNE) represents the optimal assemblage of environmental information for predicting Argentine ant distributions.

Within-region predictivity data set

The tests of occurrence predictivity within three regions (native range, Iberian Peninsula, North America) using the subsets described in *Methods* indicated quite powerful predictive ability. In fact, using the HNE environmental data sets, all six reciprocal predictions were statistically significant based on the ROC tests ($P < 0.001$). The native-range models showed the lowest AUCs (AUC subindices indicate the subset used to build the models; $AUC_{set1} = 0.62 \pm 0.06$, and $AUC_{set2} = 0.73 \pm 0.05$) in relation to the Iberian Peninsula ($AUC_{east} = 0.75 \pm 0.02$ and $AUC_{west} = 0.76 \pm 0.02$) and North America ($AUC_{east} = 0.90 \pm 0.02$ and $AUC_{west} = 0.77 \pm 0.02$), probably reflecting lower sample sizes. Omission rates (i.e., failure to predict known occurrences) were low (Table 1), suggesting that the ENMs were successfully predicting extents of occurrences in each region. Overall, the results of these tests indicate significant

TABLE 1. Statistical results of cross-prediction comparisons among distributional regions for the Argentine ant (*Linepithema humile*).

Model	AUC	Omission (%)		Commission (%)		AUC comparisons		
		>90% best	10 best	>90% best	10 best	Iberian	N. Amer.	Japan
Native area ($n = 64$)								
Native	0.7512 ± 0.0354***	10.9	0	50.8	79.3	***	***	**
Iberian	0.6125 ± 0.0375***	40.6	3.1	41.7	99.0		NS	NS
N. Amer.	0.6185 ± 0.0375***	15.6	1.6	67.0	93.4			NS
Japan	0.6098 ± 0.0375***	98.4	75.0	0	3.5			
Iberian Peninsula ($n = 341$)								
Native	0.7564 ± 0.0153***	44.3	9.7	9.0	74.8	NS	***	***
Iberian	0.8308 ± 0.0137***	14.7	3.2	26.9	53.1		***	***
N. Amer.	0.5927 ± 0.0162***	10.0	2.1	76.2	96.3			NS
Japan	0.5618 ± 0.0161***	94.1	64.8	0.7	25.1			
North America ($n = 280$)								
Native	0.7842 ± 0.0163***	40.0	7.9	8.2	82.8	NS	NS	***
Iberian	0.8371 ± 0.0149***	43.6	9.3	6.9	51.4		*	***
N. Amer.	0.8025 ± 0.0159***	5.0	0	40.6	77.6			***
Japan	0.6356 ± 0.0179***	93.2	52.9	1.2	21.5			
Japan ($n = 9$)								
Native	0.7841 ± 0.0909***	44.4	11.1	15.9	43.1	NS	NS	NS
Iberian	0.6579 ± 0.0996**	44.4	11.1	11.8	79.8		NS	NS
N. Amer.	0.7316 ± 0.0960***	22.2	0	34.4	79.8			NS
Japan	0.9880 ± 0.0256***	55.6	0	0.9	8.4			

Notes: Occurrence data from each region were used to develop ecological niche models (first column), which were then projected onto each other region (boldface side headings of first column delineating sections) for testing model accuracy using receiver operating characteristic (ROC) analysis. For each predicted region two analyses are presented: (1) general statistics as mean area under the curve (AUC) and its standard error, omission (percentage of occurrence data incorrectly predicted as absent), and commission (percentage of area predicted present) at two different thresholds (areas predicted by >90% of best-subset models and by any of 10 best-subset models, respectively); and (2) significance in the z test comparing the AUCs (three right-hand columns) among models. Asterisks indicate the significance of z tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Sample sizes represent the number of Argentine ant occurrence localities used for developing the models. All models were developed using the combined topography, normalized difference vegetation index (NDVI), and the enhanced vegetation index (EVI) environmental data set (HNE).

predictive power for modeling Argentine ant distributions in a variety of geographic contexts.

Niche comparisons among regions

All cross-predictions among distributional regions (native range, Iberian Peninsula, North America, Japan) were statistically significant in ROC tests ($P < 0.01$; Table 1). As such, a general result of these analyses is that we find no evidence that ecological niches have either evolved or have been modified by different community contexts in the species' colonization of areas worldwide over the last century (Peterson et al. 1999). However, some differences do appear between the actual predictions of different regional models (Fig. 1).

Native-range models accurately predicted known distributions of Argentine ants in each invaded region (Table 1). However, these models also suggest additional areas in which Argentine ants are not known to occur, ostensibly areas of potential future invasion. For example, projections for the Iberian Peninsula successfully predicted species' presence along southern and western coastlines and suggested the potential for expansion into the interior of the Iberian Peninsula. Similarly, these models correctly predicted known Argentine ant distributional areas along the southeastern and western coasts of North America and again highlighted interior areas as also suitable for the species. On the other hand, invaded-range models provided results somewhat different from the native-range models. For example, models based on occurrences in the Iberian Peninsula predicted potential distributional areas on the coast and along important rivers in the Iberian Peninsula, perhaps reflecting some degree of coastal bias in the occurrence data available from that region. North American and Japanese models predicted new potential areas for invasion where Argentine ants are not presently documented (e.g., northern United States and Japan, interior areas along major rivers).

Comparing AUCs of native-range-based models with those of invaded-based models projected to the native area, AUCs are significantly higher in models based on invaded areas ($P < 0.01$), suggesting that regional models vary somewhat in how they characterized the ecological niche of the species. Comparisons between the native- and invaded-based models for given regions also exhibit differences, particularly for the native area, whereas native- and invaded-based models for the Iberian Peninsula, North America, and Japan are not significantly different (Table 1). North America-based models predicted the broadest potential distributions in all areas, indeed somewhat overpredicting the actual distribution of the species. Finally, Japan-based models

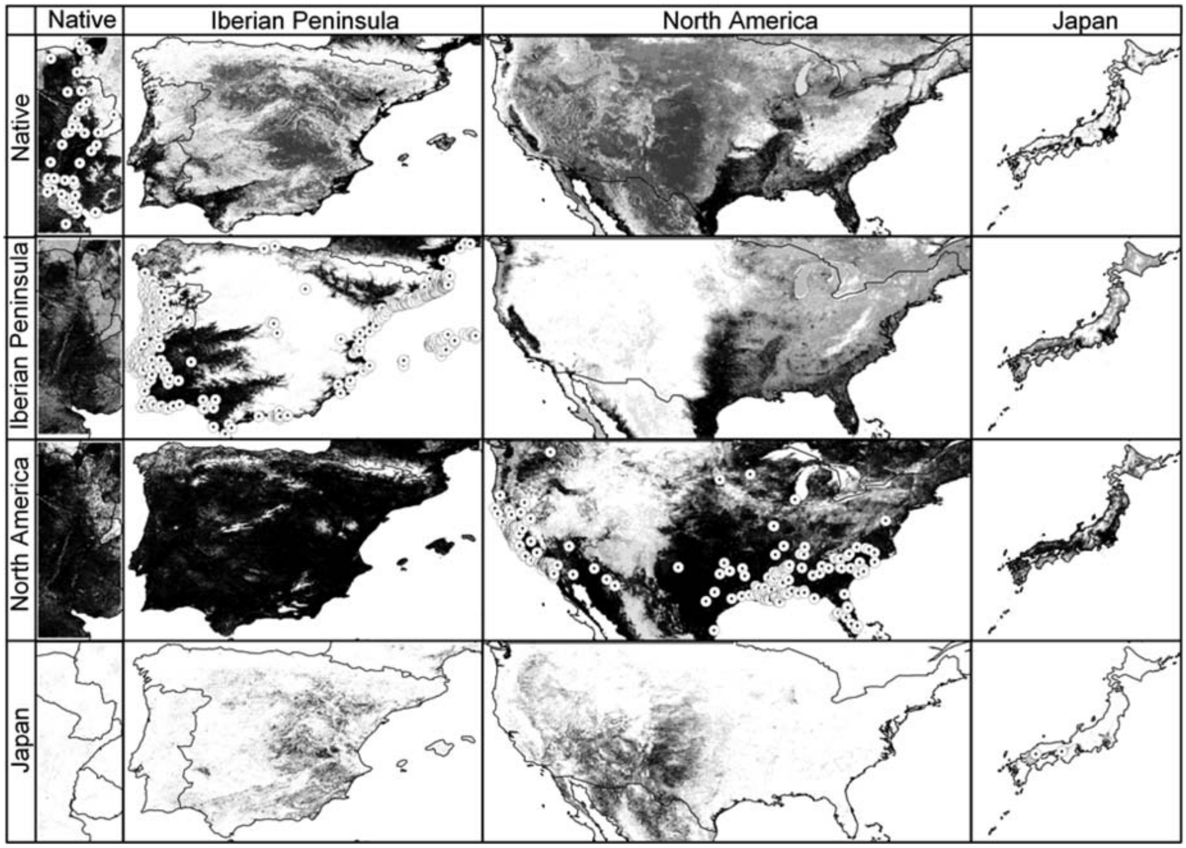

FIG. 1. Predicted distribution of the Argentine ant (*Linepithema humile*) among the native range, Iberian Peninsula, North America, and Japan. Regions used to develop models are in each row, and columns indicate the region to which the model was projected. All models were developed using the combined topography, normalized difference vegetation index (NDVI), and the enhanced vegetation index (EVI) environmental data set (HNE). Greater model agreement in predicting potential occurrence is indicated in darker shades, and dotted circles indicate occurrence data used to build models.

presented less intense and less extensive predictions in other regions, probably reflecting small sample sizes across an ecologically restricted landscape or nonequilibrium distribution in Japan.

These differences between model predictions may result from environmental differences among regions, differences in invasion biology, or differences in sampling schemes. The species' ecological niche as modeled in each area and projected to each other area can be represented in bivariate plots of the principal components summarizing environmental space, which explained 61.2% of total variation in environmental parameters in the PCA analysis. Principal components axis 1 (PC1; 49.6% variation) was correlated positively with elevation (0.585) and negatively with NDVI and EVI values (ranging from −0.653 to −0.892); the principal components axis 2 (PC2; 11.6% variation), on the other hand, was related positively with EVI of August and July (0.555 and 0.534, respectively) and negatively with NDVI of February and January (−0.593 and −0.523, respectively). In general, Argentine ant ecological niches as reconstructed in its native range, the Iberian Peninsula, and North America were quite similar (Fig. 2), but that reconstructed based on Japanese occurrences was considerably more restricted, again likely reflecting either a still-small distributional area there or limited sampling compared with other areas. In general, comparing conditions available across areas, differences observed are most likely artifacts of sampling or environmental differences among areas and not real differences in the species' ecological niche.

DISCUSSION

This study develops and compares ecological niche characteristics of Argentine ants on the species' native range and in three invaded areas. A previous study (Roura-Pascual et al. 2004) examined the species' global potential for spread based on its native-range ecological niche and suggested that the overall approach held promise for modeling this species' potential geographic distribution. This study confirms and expands the previous results by examining differences between ecological niches as reconstructed from points on native and invaded ranges at much finer resolution and with more analytical detail.

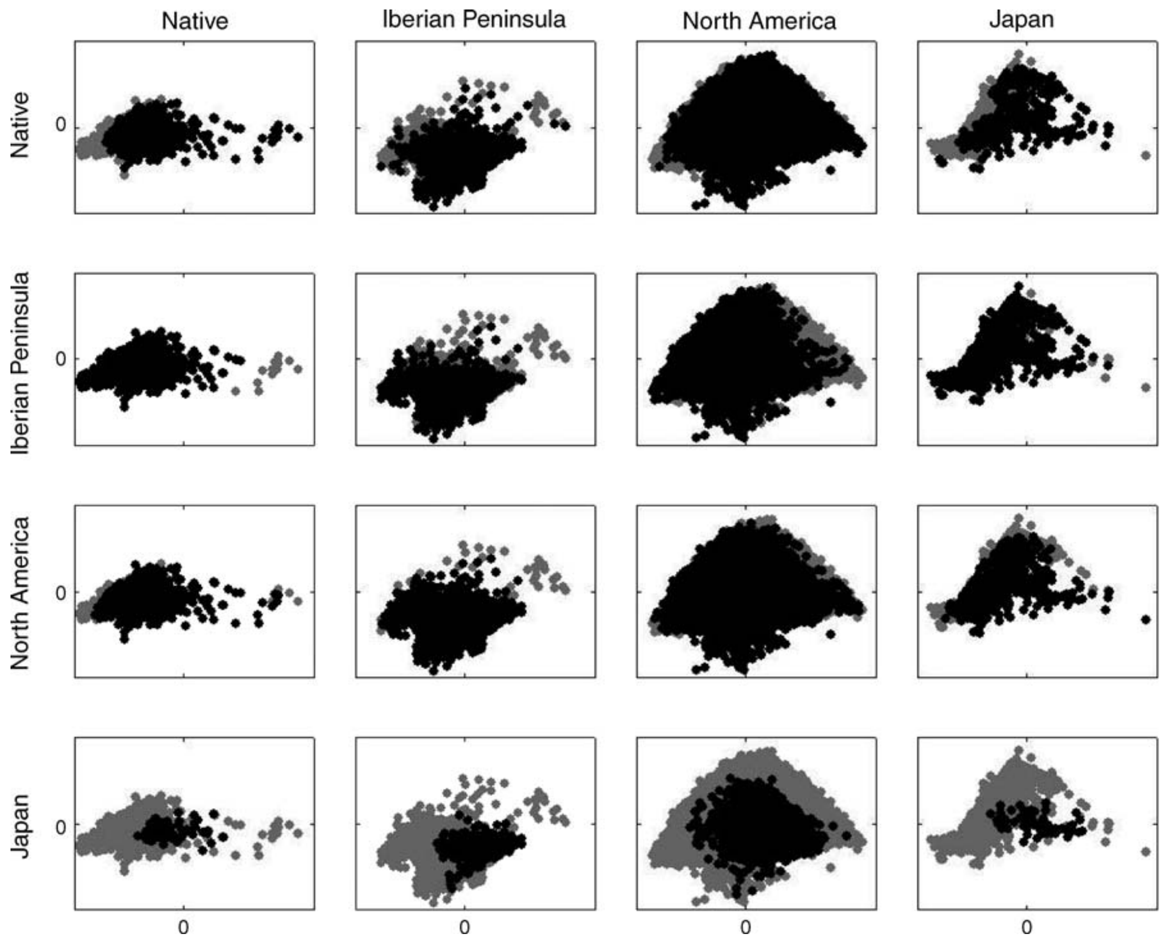

FIG. 2. Visualizations of Argentine ant niche models in ecological space, in the form of a bivariate plot of principal components 1 and 2 (PC1 and PC2), which summarize overall variation patterns in the 30 original dimensions in which we studied the species' niche. Black points indicate predicted presence, whereas gray points indicate environmental conditions present in the area but not predicted as habitable for the species. Rows indicate the region used for building models, and columns indicate the region to which models were projected.

Overall, tests assessing robustness and adequacy of the environmental and occurrence data sets employed indicated that they were sufficient for comparing native- and invaded-range ecological niches of Argentine ants. Statistical tests and visual inspections of models generated using all possible combinations of environmental data sets (step 1) suggest that those models based on vegetation indices alone predicted broader potential distributions than models including only topographic information. Although models based on NDVI and EVI together seem possibly overfit, we preferred to use both indices because they presented slight differences in their predictions, and predictions from models generated using all available environmental data (HNE) were highly accurate in the ROC tests. This result is consistent with previous studies (Holway 1998, Paiva et al. 1998, Holway et al. 2002*b*) that suggest that topographic, climatic, and habitat data are all important factors governing Argentine ant distributions.

Regarding sample sizes, our results suggest that ~60 occurrence points would be sufficient to achieve maximum predictive accuracy. Japan was excluded from these within-region analyses because of the small sample size available (Stockwell and Peterson 2002*b*). However, Japan-based models were kept in the cross-prediction analyses (step 3), so AUC values for predictions of Japanese distributional region are potentially misleading, given a decided lack of statistical power ($n = 9$ occurrences only).

The results of the cross-prediction analysis (step 3) suggest that ecological niche characteristics do not differ markedly between native and invaded ranges at the spatial and temporal scale of our analysis. As such, these results complement those of previous studies (Peterson 2003) in demonstrating general conservatism of species' ecological niches. Within this general result of ecological niche stability among Argentine ant populations, however, we did observe some region-to-region variation in model results (Fig. 1 and Table 1). These variations may be the result of vagaries of sampling, limitations of the modeling tools, environmental difference between regions, or subtle differences between ecological niches of regional populations. Some reasons for variation caused by modeling limitations are explored here.

Data-input-related errors, such as occurrence data providing an inadequate sampling of environmental conditions and/or biased or insufficient environmental data, may introduce model-to-model variation. Our occurrence data come principally from museum specimen label data and personal collections (rather than from planned sampling schemes), so sampling biases can occur. This may be problematic if species' presence is recorded from a building (such as greenhouse) where it may persist regardless of environmental conditions (for example, Argentine ant records from the extreme northern United States). The GARP controls these biases to some degree by rasterizing (to reduce redundancy due to duplicate or close locations) and balancing sample size in presence and pseudo-absence data sets (Stockwell and Peterson 2002*a*). Furthermore, numbers of occurrences were clearly sufficient to prepare models, except for Japan, from which we had limited information. Therefore, GARP appears capable of controlling sampling biases in occurrence data and providing accurate predictions of Argentine ant distributions.

Only a reduced number of environmental variables is available at fine resolutions for ENM development, which limits predictive capacity of models (Peterson and Cohoon 1999). In this sense, the lack of human-related data at fine resolution impedes taking into account anthropogenic influences (e.g., increased water availability from urban and agricultural sources), which may be a better predictor of Argentine ant establishment and spread than climate envelopes in some arid environments (Holway et al. 2002*b*). We here resolved this environmental data "gap" via use of remote sensing data, which appears to be an excellent surrogate for land cover and climatic data sets in predicting Argentine ant distribution (Egbert et al. 2002).

Models may need to take into account biotic interactions as well. In this study, we took into account only abiotic variables and omitted effects that other species might have on Argentine ant distribution and ecology. In the native range, natural enemies and a species-rich and highly competitive ant fauna may well limit Argentine ants from occupying all suitable areas (Holway et al. 2002*a*, Heller 2004); to the extent that this limitation can act in ecological space and adjust the ecological profile of the species, it may influence our results (Case et al. 2005). Similarly, in North America, another highly invasive ant species, *Solenopsis invicta*, may reduce the success of Argentine ants (Wilson 1951, Fitzpatrick and Weltzin 2005), although this idea remains to be tested. Nonetheless, given the high predictive ability of our models among regions, these biotic effects are probably limited in their scope and influence.

The pixel resolution of environmental data (1×1 km) may also cloud some finer-scale variations in the species' ecological niche that are not detectable at the spatial scale of our analysis (A. Guisan, *personal communication*). Because the influence of each environmental variable in determining the species' niche is scale dependent, different degrees of ecological niche variation can arise among populations, depending on the spatial resolution of analyses (Wiens 1989). Nevertheless, these possible finer geographical variations in niches do not alter the accuracy of our models for predicting Argentine ant niches at the spatial resolution of our analysis.

Differences in the range of ecological conditions (limits of ecological space) from region to region may further complicate the situation (Peterson and Holt 2003). That is, if different regions differ in the "universes" of ecological conditions that they present (Fig. 2), models built in areas presenting limited conditions may be unable to generalize to areas that are more ecologically diverse. An example of this effect is shown in Japan-based models, which seemed to have difficulty in anticipating the species' potential distribution in other areas.

Dispersal is an important factor that can influence a species' pattern of invasion (Higgins and Richardson 1999, With 2002). Because Argentine ants commonly spread through human-mediated jump dispersal, natural limitations to dispersal such as ecological barriers may not be as relevant and have minor influences on their distribution at the spatial scale of our analysis (Suarez et al. 2001).

Invasion history needs to be taken into account in predicting the species' distribution (Williamson 1996). The Argentine ant "invasion" is likely not complete, and thus the species may be out of equilibrium in some regions (Holway 1998, Casellas 2004). As such, occurrence information from some invaded regions may be biased or limited geographically and possibly ecologically, simply reflecting that the species has not reached those areas yet. Such could be the situation in Japan and unsampled areas of potential presence in other regions; future studies should be addressed to determine the actual geographic distribution (i.e., areas of both presence and absence of the species) and the degree of spread of Argentine ants across regions.

Alternately, real ecological niche differences (that is, the species occupies a different ecological space in two areas, although both areas present the full range of conditions) could result from evolutionary or ecological shifts in the characteristics of the species. In some invasive ants, such as the red-imported fire ant (*Solenopsis invicta*), the little fire ant (*Wasmannia auropunctata*), and the Argentine ant, introduced populations are known to differ from native populations in behavior and colony structure (Ross et al. 1996, Holway and Suarez 1999, Tsutsui et al. 2000, LeBreton et al. 2004). For example, in Argentine ants, differences among populations in the degree of unicoloniality (Tsutsui and Suarez 2003, Buczkowski et al. 2004, Heller 2004, Holway and Suarez 2004), the absence of strong competitors and parasites in new environments, and evolutionary adaptation to new environments could influence invasion success and form the basis for ecological differentiation between native and introduced populations. As ecological differences between native-range and invaded-range areas as measured in this study appear minor, we suspect that these phenotypic differences relating to ecological tolerance of abiotic conditions may not be broadly manifested or pervasive at the coarser spatial scales of our analyses.

More generally, this study has demonstrated two important points. (1) We proved the utility of remotely sensed data in predicting potential geographic distributions of invasive species (Peterson 2003). (2) We also found that ecological niche characteristics of Argentine ants are not markedly different among distributional areas, suggesting that ecological, behavioral, and other differences observed in detailed single-site studies are not manifested at broader spatial scales.

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