

Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change

Núria Roura-Pascual^{1*}, Andrew V. Suarez², Crisanto Gómez¹, Pere Pons¹, Yoshifumi Touyama³, Alexander L. Wild⁴ and A. Townsend Peterson⁵

¹Departament de Ciències Ambientals, Universitat de Girona, Campus de Montilivi, 17071 Girona, Catalonia, Spain

²Departments of Entomology and Animal Biology, School of Integrative Biology, University of Illinois, 320 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA

³Department of Environmental Studies, Faculty of Integrated Arts and Sciences, Hiroshima University, Higashi-Hiroshima, Japan

⁴Departament of Entomology, University of California at Davis, One Shields Avenue, Davis, CA 95616, USA

⁵Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS 66045, USA

Determining the spread and potential geographical distribution of invasive species is integral to making invasion biology a predictive science. We assembled a dataset of over 1000 occurrences of the Argentine ant (*Linepithema humile*), one of the world's worst invasive alien species. Native to central South America, Argentine ants are now found in many Mediterranean and subtropical climates around the world. We used this dataset to assess the species' potential geographical and ecological distribution, and to examine changes in its distributional potential associated with global climate change, using techniques for ecological niche modelling. Models developed were highly predictive of the species' overall range, including both the native distributional area and invaded areas worldwide. Despite its already widespread occurrence, *L. humile* has potential for further spread, with tropical coastal Africa and southeast Asia apparently vulnerable to invasion. Projecting ecological niche models onto four general circulation model scenarios of future (2050s) climates provided scenarios of the species' potential for distributional expansion with warming climates: generally, the species was predicted to retract its range in tropical regions, but to expand at higher latitude areas.

Keywords: world distributional prediction; ecological niche; GARP; global climate change; *Linepithema humile*; biological invasions

1. INTRODUCTION

Global environmental change alters the spatial distribution of physical conditions, habitats and species on Earth (Chapin *et al.* 2000). With widespread ecological impacts, biological invasions are a significant component of human-caused global environmental change (Vitousek *et al.* 1997). Understanding the biology of invasive species and their potential geographical distributions is essential to anticipating their large-scale and long-term effects (Tsutsui *et al.* 2001). Despite the widely acknowledged need for making invasion biology a more predictive science (Perrins *et al.* 1992; Carlton 1996; Kareiva 1996; Williamson 1996; NAS 2002), relatively few studies have modelled the potential ecological distribution of invasive species (Mack *et al.* 2000; Hulme 2003; Peterson 2003).

Invasive ants have many negative impacts on ecological communities in their introduced ranges (Holway *et al.* 2002a), making them key in conservation efforts (McGlynn 1999; Holway *et al.* 2002a). The Argentine ant (*Linepithema humile*) is a widespread invader (see <http://www.issg.org/database>); native to South America, it is now established in at least 15 countries on six continents and many oceanic islands (Suarez *et al.* 2001). Although associated with human-modified habitats throughout its non-native range, the Argentine

ant can also colonize natural areas with low anthropogenic disturbance (De Kock & Giliomee 1989; Holway 1998; Suarez *et al.* 2001; Gómez *et al.* 2003). Worldwide, *L. humile* has impacted native ant faunas, leading to changes in arthropod communities, ant-vertebrate interactions, and ant-plant relationships, as well as economic effects, such as food contamination and damage to infrastructure (Bond & Slingsby 1984; Cole *et al.* 1992; Human & Gordon 1996; Suarez *et al.* 1998, 2000; Vega & Rust 2001; Holway *et al.* 2002a; Gómez & Oliveras 2003; Touyama *et al.* 2003). Despite the numerous studies of *L. humile*, little research has focused on its ecological and geographical distribution at broad spatial scales (Tsutsui *et al.* 2000, 2001; Suarez *et al.* 2001; Hartley & Lester 2003; Wild 2004), and no study has yet assessed the probable changes in its global distributional potential associated with global climate change.

We use the Argentine ant as a model system to develop predictive models of an invader's potential global range. We compiled a dataset of 1000+ known occurrences to examine the Argentine ant's potential geographical distribution, and explore the consequences of global climate change on its distribution under various scenarios of climate change for the next 50 years.

2. MATERIAL AND METHODS

Ecological niche models are based on non-random correlations between known occurrences of species and environmental datasets

* Author for correspondence (nuri.roura@udg.es).

that describe parameters ostensibly related to the dimensions of the ecological niche of the species. We developed ecological niche models for Argentine ant potential distributions based on two independent environmental datasets; differences in their origin and resolution make combination difficult, but similarities in results based on such distinct datasets provide an excellent indication of robustness of results. Occurrence data were used to determine that the species' native distribution was centred along major river systems in northeastern Argentina and southern Paraguay (Tsutsui *et al.* 2001; Wild 2004). This area was carefully delineated to avoid accidental inclusion of related species of *Linepithema* (Wild 2004).

(a) Datasets

Overall, we used 1007 occurrence points drawn from data associated with specimens in natural history museums and personal collections; scientific literature; and onsite field surveys (see electronic Appendix A, available on The Royal Society's Publications Web site). Models were based on 67 occurrence points that are putatively from the species' native range; because of the potential for misidentifications even in the native range, we used only those localities visited personally by the authors and/or verified in ongoing taxonomic research by one of the authors (Wild 2004). A set of 940 occurrence points from other areas (i.e. invaded areas) was withheld from model building, and used only for an extrinsic evaluation of final predicted potential invasive distributions (as not all of these localities have been reviewed personally by the authors, some misidentifications may exist). Likewise, 31 sites that represent putative absences within or close to the native range established in onsite visits by the authors, or in detailed faunal studies, were used in tests of model accuracy. All occurrence data are provided in electronic Appendix B.

The two environmental datasets (in the form of digital maps, or 'coverages') differed in the variables summarized, spatial resolution, and interpretability. The first, with relatively coarse spatial resolution, included 15 coverages summarizing aspects of topography (elevation, topographic index, slope, aspect, flow direction and flow accumulation, from the US Geological Survey's Hydro-1K dataset; <http://edcdaac.udgs.gov/topo30/hydro/>, native resolution 1 km × 1 km) and climate (annual means of diurnal temperature range; frost days; precipitation; maximum, minimum and mean temperatures; solar radiation; wet days; and vapour pressure; for 1960–1990 from the Intergovernmental Panel on Climate Change; <http://www.ipcc.ch/>, native resolution 50 km × 50 km). To minimize conflicts in scale between topographic and climatic data, we conducted analyses at an intermediate resolution (10 km × 10 km). As several of the coverages derived from the topographic data (e.g. topographic index, flow direction, and flow accumulation) were not available for Australia, we developed separate (but parallel) models for that continent simply omitting the coverages that were lacking.

The second dataset, with a somewhat finer overall native resolution, included 18 coverages: the same topographic variables listed above, plus monthly remotely-sensed data layers summarizing the Normalized Difference Vegetation Index (NDVI) as measured by the Advanced Very High Resolution Radiometer (AVHRR) satellite (<http://glcf.umiacs.umd.edu/data/landcover/>; native resolution 8 km × 8 km) for 1999, matching the modal date of the occurrence data used. Such composites of AVHRR imagery and topographic data have been shown to be effective data inputs for fine-scale predictions of species' distributions (Egbert *et al.* 2002; Peterson *et al.* 2004). Because AVHRR data were unavailable at high latitudes, we eliminated such (greater than 60°) areas from consideration. To account for differences in summer–winter

timing between Northern and Southern Hemispheres, and given the monthly nature of the AVHRR data, we shifted Southern Hemisphere monthly data by six months, thereby aligning northern and austral summers and winters appropriately.

All of the manipulations described below except climate-change projections, which were possible only for climate-based analyses, were repeated for both environmental datasets. Throughout, we refer to the two datasets as 'climate' data and 'NDVI' data, respectively. Models were developed across central–eastern South America, and projected worldwide to explore geographical implications.

(b) Niche modelling

Our approach is based on modelling species' ecological niches (Peterson *et al.* 2002b, 2003; Stockwell & Peterson 2002), which have been shown to constitute long-term stable constraint on species' potential geographical distributions (Peterson *et al.* 1999; Martinez-Meyer 2002; Peterson 2001, 2003). Ecological niches are herein defined as the set of conditions under which a species is able to maintain populations without immigration (Grinnell 1917, 1924). Several avenues of research have demonstrated widespread evolutionary conservatism in niche characteristics (Peterson *et al.* 1999; Martinez-Meyer 2002), allowing accurate predictions of invasive species' potential distributions (Peterson 2003). Ecological niche characteristics represent but one factor in the complex phenomenon of invasions, which includes (i) dispersal and colonization of new areas, (ii) establishment of non-native populations, (iii) the ecological appropriateness of new areas (i.e. does the area fit the species' niche requirements?), and (iv) population expansion and spread across these areas; therefore, although ecological niche modelling cannot explain the entire invasion process, it does provide an excellent assessment of the potential geographical dimensions of the phenomenon (Peterson 2003).

Our approach consisted of five steps. (i) Model the ecological niche requirements of the species based on known occurrences on the native distribution area of the species. (ii) Test the accuracy of the native-range predictions. (iii) Project the niche model onto other regions to identify areas susceptible to invasion. (iv) Test to validate predictions in other regions. (v) Project niche models onto scenarios of future climate change to predict potential distributional shifts (Peterson *et al.* 2001, 2002a; Peterson & Shaw 2003).

The software tool used for niche modelling was the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Peters 1999). GARP uses a genetic algorithm to search for non-random associations between environmental variables and known occurrences, as contrasted with the environmental characteristics of the overall study area. Occurrence points (as longitude–latitude coordinates) are mapped onto a spatial grid, and combined with environmental variables (in the form of digital maps, or 'coverages') in an evolutionary computing environment to develop a model of the species' ecological niche. The resulting model is then used to classify the entire study area to identify areas modelled as suitable. Although these environmental variables cannot represent all possible ecological-niche dimensions, they probably represent, or are correlated with, many influential ones in delineating the species' potential distribution. Previous tests of GARP have shown successful predictions of distributional phenomena for numerous taxa and regions (Peterson 2001; Peterson *et al.* 2002a; Peterson & Kluza 2003).

Available occurrence points (67, in the present case) are resampled with replacement to create a population of 1250 presence

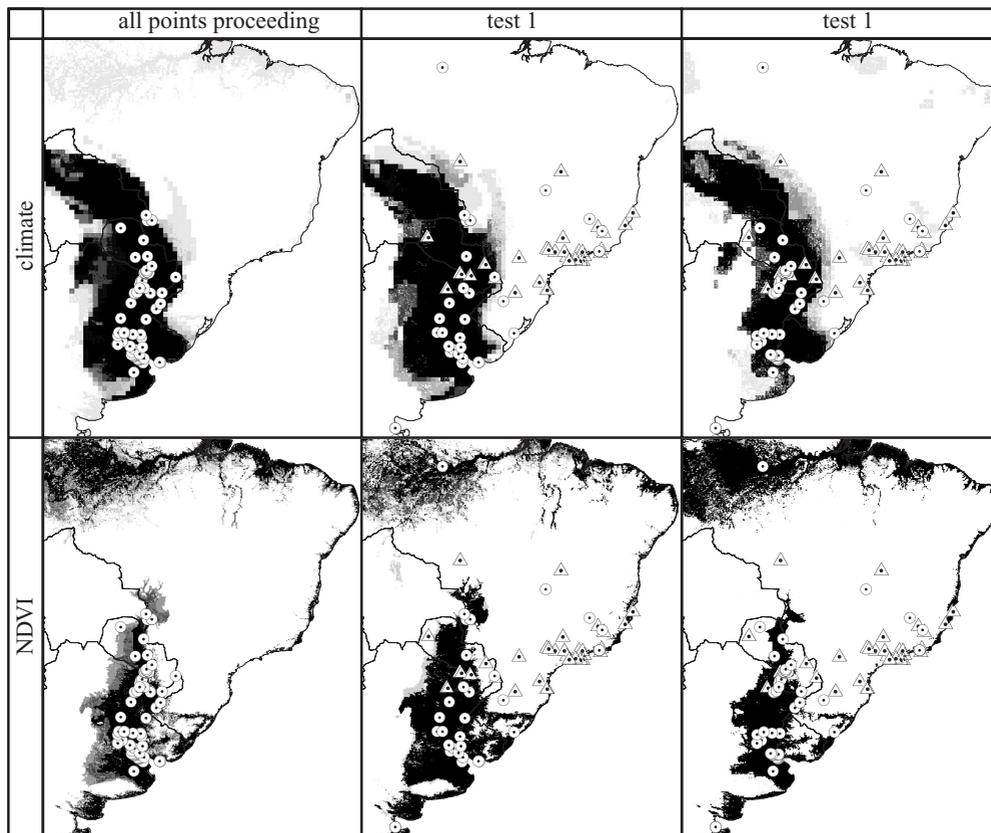


Figure 1. Illustration of tests used to assess model predictivity for two environmental datasets (climate and NDVI). Occurrence data for the Argentine ant in the native range were divided into two categories depending on their position in relation to a grid of $2^{\circ} \times 2^{\circ}$. Independent occurrence data are overlaid in each prediction, presences in circles and absences in triangles. The first column presents predictions based on all native occurrence data combined, and second and third columns present predictions based on the two reciprocal spatial subdivisions of the available native occurrence data, with appropriate test dataset overlaid. Darker shading indicates greater model agreement in predicting potential Argentine ant presence.

points; an equivalent number of points is resampled from the population of grid squares ('pixels') from which the species has not been recorded. These 2500 points are divided equally into training (for creating models) and testing (for evaluating model quality) datasets (Anderson *et al.* 2003). Resampling occurrence points reduces the effects of sampling biases, such as omission, spatial bias, or imbalances in available occurrence data (Stockwell & Peters 1999).

Models are composed of a set of conditional rules developed through an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules, etc), and applied to the training dataset. Then, a rule is developed by several means mimicking DNA evolution: point mutations, deletions, crossing over, etc., to maximize predictive accuracy. Rule accuracy is evaluated through the testing data, as a significance parameter based on the percentage of points correctly predicted as present or absent by the rule. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the final rule-set. The algorithm runs either 1000 iterations or until addition of new rules has no effect on predictive accuracy. The final rule-set, or ecological niche model is then projected onto a digital map to identify a potential geographical distribution (Stockwell & Peters 1999).

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) (Fielding

& Bell 1997). To achieve the highest predictive accuracy and simultaneously achieve a most general result (i.e. able to be extrapolated to other conditions and regions), before modelling, we reduced each environmental dataset to just those coverages contributing positively to model quality using a jack-knife procedure (Peterson & Cohoon 1999). We systematically omitted one to three coverages at a time, and calculated Pearson product-moment correlations between inclusion-exclusion of a particular coverage and omission error in each resulting model (Peterson & Cohoon 1999; Peterson *et al.* 2003). Coverages presenting a positive correlation of $r > 0.08$ were removed from further analysis, and modelling thus focused on those data coverages that contributed positively to models having low omission rates.

Because GARP does not produce unique solutions, we followed recently published best practices approaches to identifying an optimal subset of resulting replicate models (Anderson *et al.* 2003). For each analysis, we developed 1000 replicate models; of these models, we retained the 200 models with lowest omission error. Finally, we retained the 100 models with moderate commission error (i.e. we discarded the 100 models with area predicted present showing greatest deviations from the overall median area predicted present across all models). This 'best subset' of models was summed to produce final predictions of potential distributions.

To validate our model predictions, we compared their ability to predict independent sets of test points with that expected under random models by two methods. In the native distributional area in

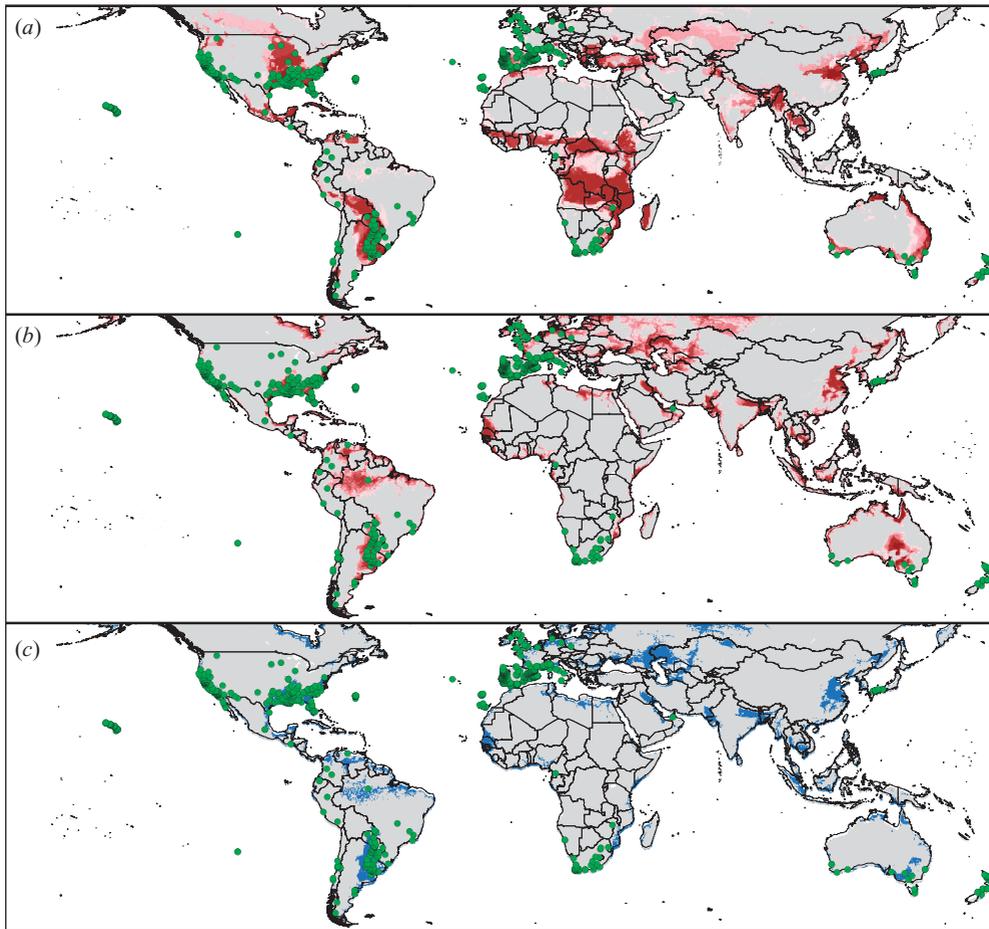


Figure 2. Worldwide predicted potential distribution for the Argentine ant, based on native-range ecological niche models based on: (a) climate data, and (b) NDVI datasets; (c) coincident areas identified in both modelling efforts (in blue). Occurrences of the species in both the native and the invaded range are plotted as green circles. Darker shading of red indicates greater model agreement in predicting potential Argentine ant presence.

which data on both presences and absences were available, we used the more robust kappa approach (Congalton & Green 1999; Jenness & Wynee 2004). We had 31 absence points and 75 presence points, including the 67 native range points plus eight presences from adjacent areas that apparently represent introductions. We calculated the KHAT statistic using a custom ArcView 3.2 extension (Jenness & Wynee 2004). Because test results depend critically on how occurrence points are divided into training and testing datasets (Fielding & Bell 1997), we used a checkerboard approach that presents a maximum challenge to the model—prediction into areas from which no occurrence information was available (Peterson & Shaw 2003). Native distribution localities were classified into two categories depending on their location on a $2^{\circ} \times 2^{\circ}$ checkerboard grid. Ecological niche models based on localities in one category were used to predict the distribution of the other occurrence category and vice versa.

We then projected these validated native-range ecological niche models onto landscapes worldwide to evaluate the species' invasive potential. On invaded distributional areas, given that absence data were not available, models were validated by χ^2 -tests (Peterson & Shaw 2003; Peterson *et al.* 2003) that incorporate dimensions of correct prediction of both presences (based on independent test data) and absences (based on expected frequencies) (Stockwell & Peters 1999; Anderson *et al.* 2003). Here, random expectations were calculated as the product of the proportional area predicted present and the number of test presence points. Observed

frequencies of correct and incorrect predictions of presence were then compared using a χ^2 -test (1 d.f.). Given that sampling of invaded distributions was highly biased towards certain regions (western Europe, North America), in addition to worldwide tests, we perform more conservative χ^2 -tests specifically in those densely-sampled regions, buffering known occurrences by 500 km to determine areas for tests.

Finally, we developed ecological niche models for extrapolation to future climates to predict the species' potential future distribution. Because fewer environmental dimensions are available for changed-climate scenarios, these models were, of necessity, based on a somewhat reduced set of climate coverages (precipitation, and minimum, mean and maximum temperature) plus topography. Once again, to reduce dimensionality of analyses, we performed a jack-knife manipulation. Ecological niche models developed were projected onto future climate datasets (2050s) (Peterson *et al.* 2001) derived from two general circulation models: CGCM2 developed at the Canadian Center for Climate Modelling and Analysis, and HadCM3 at the Hadley Center for Climate Prediction and Research. Two emissions scenarios (A2 and B2) were used: B2 scenarios (CGCM2B2 and HadCM3B2) assume $0.5\% \text{ yr}^{-1}$ CO_2 increase and incorporate sulphate aerosol forcing, making them relatively conservative, whereas A2 scenarios (CGCM2A2 and HadCM3A2) assume a $1\% \text{ yr}^{-1}$ CO_2 increase and do not take into account effects of sulphate aerosols, and are thus more severe.

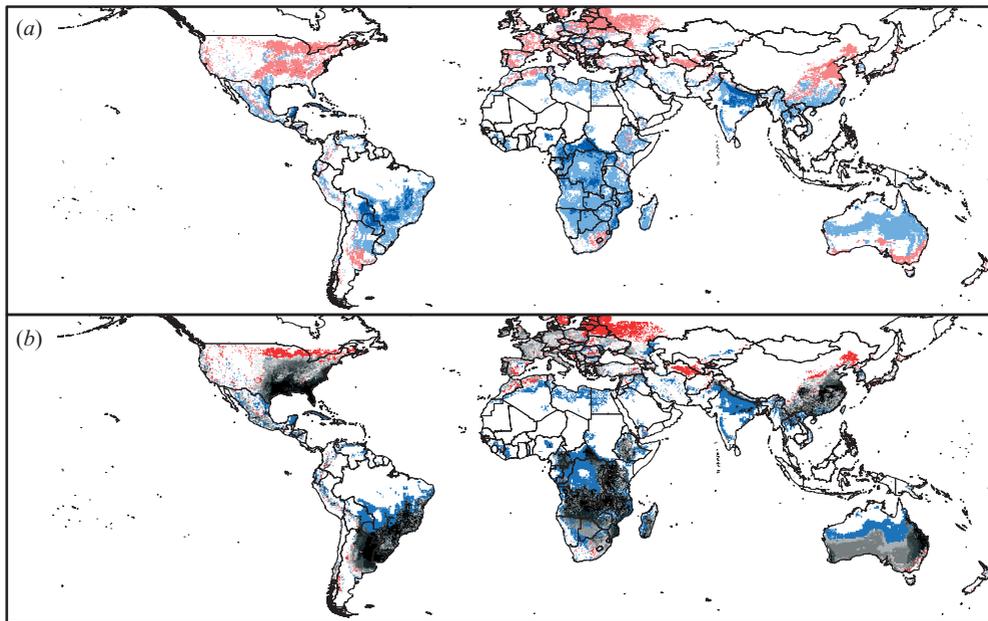


Figure 3. Worldwide predicted changes in potential distributional area for the Argentine ant between the present time and 2050. (a) Difference maps (future suitability values minus present suitability values), showing expected changes in climatic suitability for Argentine ants: red shades indicate areas predicted to improve for Argentine ants, whereas blue shading indicates areas predicted to worsen for the species. (b) Areas predicted to become newly habitable or non-habitable for the Argentine ant: the greyscale indicates present-day potential presence (darker shades greater confidence), red indicates areas predicted to become habitable but not currently habitable, and blue indicates areas currently habitable but predicted to become non-habitable in the future. Maps represent the average predictions of four scenarios of global climate change: HadCM3A2, HadCM3B2, CGCM2A2 and CGCM2B2.

3. RESULTS

(a) Native distribution

Native-distribution occurrence points were distributed principally in northern Argentina and southern Paraguay along major river systems (Río Paraná, Río Paraguay, and Río Uruguay). The jack-knife manipulation for the climate data led us to exclude seven coverages, leaving minimum and mean annual temperatures, precipitation, diurnal temperature range, wet days, flow accumulation and flow direction for modelling (none with inclusion strongly positively associated with increased omission error). Best-subsets models developed based on these datasets predicted fairly continuous Argentine ant distribution from eastern Bolivia to Uruguay, through northeastern Argentina, Paraguay and southern Brazil (figure 1).

For the NDVI dataset, the jack-knife manipulation identified the following coverages for further analysis: elevation, topographic index, and NDVI coverages for January, March, April, July, August and October (none with inclusion strongly positively associated with omission error). Best-subsets NDVI-based models predicted smaller native-range areas (7–9% smaller areas depending on cut-off used for presence) than the climate-based models.

Both models predicted well the species' distribution in non-sampled regions based on the two reciprocal checkerboard tests. Test sample sizes available were 44 and 23 for the two reciprocal tests. Overall accuracy measures for the two climatic models were 84–87%, and KHAT values were 0.68–0.74; for NDVI models, accuracies were 87–89%, and KHAT values 0.71–0.75. Because KHAT ranges from –1 to +1, these results suggest excellent agreement between model predictions and actual distributional patterns. Comparisons of kappa statistics and associated variances

between the two environmental datasets indicated that they were not significantly different ($p > 0.3$). As such, these two environmental datasets can be considered complementary, producing approximately equal classifications.

(b) Invaded distribution

Given that ecological niche models based on both environmental datasets yielded highly accurate predictions of the native distribution, we projected them worldwide. For climate-based models, areas outside the native distribution with the most suitable conditions were the west coast and southeast of the United States, Mediterranean coast, central and southern Africa, western Madagascar, parts of central Asia (e.g. Kazakhstan), western India, a band from northeastern India to Thailand, northeastern China, Korea, southern Japan, coastal Australia and New Zealand (figure 2a). NDVI-based models predicted similar patterns of potential distribution, although generally in more restricted areas. Climate-based models predicted areas of potential distribution in the central United States, northern Bolivia and central Africa, at variance with NDVI-based models, whereas NDVI-based models predicted areas at northern latitudes, along the Amazon River, and in central Australia at variance with the climate-based models (figure 2b). Coincident areas in predictions of both climatic and NDVI models are shown in figure 2c.

Validations of invaded-range predictions in densely sampled regions (United States and western Europe) and worldwide were uniformly significantly better than random expectations (χ^2 -tests, all $p < 10^{-7}$; table 1). Hence, this set of tests indicates that the worldwide projection of the native-range ecological niche model had considerable predictive power for distributional phenomena in this species as an invasive species. Based on present knowledge of the species,

Table 1. Summary of statistical tests of model predictions for the whole world and for two densely sampled regions, based on two sets of environmental data: climate and NDVI.

(Tests were performed for areas predicted by >90% of best-subsets models (first row of each region) and by any of 100 best-subsets models (second row of each region). North America and Western Europe test areas were analysed only for areas within 500 km of test occurrence data. prop. area, predicated area/total area of the region.)

climate dataset								
	prop. area	test <i>N</i>	obs. correct	obs. incorrect	exp. correct	exp. incorrect	χ^2	<i>p</i>
world	0.084	787	589	198	257	530	636.8	< 10 ⁻¹⁰⁰
	0.348	787	257	530	54	733	828.6	< 10 ⁻¹⁰⁰
North America	0.234	266	200	66	141	125	52.8	< 10 ⁻¹²
	0.530	266	101	165	62	204	31.3	< 10 ⁻⁷
Western Europe	0.047	328	274	54	143	185	211.0	< 10 ⁻⁴⁷
	0.044	328	83	245	16	312	308.3	< 10 ⁻⁶⁸
NDVI dataset								
world	0.066	1007	520	487	58	949	3922.4	< 10 ⁻¹⁰⁰
	0.208	1007	258	749	18	989	3189.7	< 10 ⁻¹⁰⁰
North America	0.085	293	176	117	40	253	527.9	< 10 ⁻¹⁰⁰
	0.195	293	94	199	18	275	349.6	< 10 ⁻⁷⁷
Western Europe	0.128	451	233	218	81	370	350.6	< 10 ⁻⁷⁷
	0.346	451	99	352	30	421	171.1	< 10 ⁻³⁸

predicted areas in northern latitudes (principally in NDVI predictions, and apparently caused by inclusion of topographic variables, given tests with and without this suite of variables) are not reliable. Likewise, areas of under-prediction (i.e. where predictions are negative but the species is known to be present) are minor, and correspond to urban localities where the species' presence may be made possible by the subsidy of human presence. Although predictions in some areas underestimated or overestimated the species' invasive potential, their ability to identify key distributional areas was clearly much better than that of random models.

(c) *Future potential distributions*

For development of future-climate predictions, we performed the jack-knife manipulation to reduce the dimensionality of models: coverages retained for analysis were minimum and mean annual temperature, precipitation, slope, and flow direction (inclusion of each was negatively associated with omission error). Given the coarser sample-size considerations resulting from the coarser resolution of the environmental datasets for future climates, we could validate these present-day native-range predictions only using χ^2 -tests—models were significantly more accurate than random models ($p < 10^{-3}$). Projecting these models onto the four general circulation model scenarios of future climates, *L. humile* was generally predicted to experience worsening conditions in the Tropics, but improving conditions at higher latitudes (figure 3). Overall, the spatial extent of the spatial projection of the species' ecological niche is expected to undergo a moderate (11–15%) reduction under all four future scenarios (figure 3).

4. DISCUSSION

The accuracy of models developed for the potential distributions of species depends on available sample sizes for model building (Stockwell & Peterson 2002), and on the complexity of the environmental datasets (Peterson & Cohoon 1999). In this case, excellent predictive accuracy

was achieved with models based on five to seven coverages. Differences in the final environmental coverages retained for each model depend on the nature of the ecological niche approach, wherein the combination of ecological parameters determines the potential distribution of the species instead of each environmental parameter alone. This result is consistent with previous studies (Peterson & Cohoon 1999; Stockwell & Peterson 2002). In general, at least for this species, these results suggest that 67 native-range localities were quite sufficient for modelling and predicting distributional phenomena.

Differences between the predictions developed for the native range reflect the differences between the two environmental datasets (climate versus NDVI) used for modelling. Predictions based on NDVI data are more restricted spatially than predictions based on climate data, probably reflecting the greater detail in such remotely sensed data. Studies of factors governing Argentine ant invasions (Way *et al.* 1997; Holway 1998; Human *et al.* 1998; Paiva *et al.* 1998; Suarez *et al.* 2001; Holway *et al.* 2002b) suggest that both climatic and topographic constraints are important in determining its distribution, but that other factors such as vegetation type, soil type, or perturbation of habitat may also be limiting (Paiva *et al.* 1998). For this reason and according to our results, we take both sets of predictions into account, and consider areas predicted by both models as the probable native distribution of the Argentine ant (figure 1c).

In northern Argentina and southern Paraguay, *L. humile* is almost always found along major river systems. They can be found in both disturbed and undisturbed areas, with highest densities along floodplains, in riparian areas, and on riverine beaches (Wild 2004). Our models nevertheless suggest the possibility of a broader distribution in its native range than is presently appreciated. Invaded-range predictions also indicate a broader potential distribution than is currently appreciated. Despite its widespread occurrence, many areas still remain vulnerable to invasion by Argentine ants (if they are not already there but undetected).

Especially important are areas where few or no records of Argentine ants are known, particularly northern South America and the Caribbean, parts of the Mediterranean, eastern Europe, tropical coastal Africa, Madagascar, south-east Asia, India, China, northern Australia and many oceanic islands. These predictions coincide with those by S. Hartley *et al.* (personal communication) on a coarse scale.

Our identification of new potential sites of invasion demonstrates the utility of our approach as a tool for the prevention of new infestations. Given that efforts to eradicate Argentine ants have almost no success once the species is established (Krushelnycky & Reimer 1998), these areas should be vigilant in preventing the introduction of this species through improved quarantine measures or other means. That predicted potential areas exceed actual distributional areas can result from remaining invasive potential, but also from insufficient sampling, recent invasion, or the existence of additional factors that restrict distributions (e.g. existence of allopatric sister species, interspecific competition, previous extinctions and limited dispersal abilities; Peterson 2003). Specifically, for the native range, areas lacking occurrence data can probably be explained by insufficient survey, or possibly to the presence of related species (Tsutsui *et al.* 2001; Wild 2004) that could represent potential competitors. For these reasons, a species' potential distribution is generally more extensive than its actual distribution (Peterson *et al.* 2002b; Peterson 2003). A better understanding of how these processes determine Argentine ant distributions would allow a better understanding of details of the distributional ecology of the species. Moreover, anthropogenic factors may also result in a lack of concordance between actual and predicted distributions of invasive species. For example, the success of Argentine ants in California has been tied to increased moisture levels associated with urban and agricultural runoff (Holway *et al.* 2002b). Modelling approaches, such as those employed here, do not take into account human-related disturbances and in that way can underestimate a species' potential distribution. Approaches that incorporate land use, water supplementation or other anthropogenic factors may not only have increased predictive power, but may also provide insight to specific factors responsible for detailed distributional phenomena.

In relation to global warming, our predictions suggest a general reduction of potential distribution areas for *L. humile*, particularly in the Tropics. However, some higher latitude areas are predicted to become more suitable for invasion (East Asia, northeastern United States, broader areas around Mediterranean and Caspian Seas, southern Africa, and southern Australia). Modelling influences of global climate change on a species' potential distribution presents some initial limitations: predicted distributions of species are based on climatic envelopes, not taking into account the influence of dispersal, source-sink dynamics, and species interactions (Davis *et al.* 1998; Peterson *et al.* 2001). Despite these limitations and the lack of knowledge on how *L. humile* responds to climate change (adaptation to the new ecological characteristics, dispersal to track its ecological niche, etc.), our analyses represent a first step towards understanding the influences of global climate change on the potential distribution of *L. humile*, and indeed one of the very first applications of ecological

niche modelling techniques to the challenge of anticipating changes in the invasive potential of species. More generally, given that changes in species' distributions alter global biodiversity (Chapin *et al.* 2000; Sala *et al.* 2000), species' invasion appears as a primary threat resulting from global climate change. In this sense, studies identifying potential new areas for invaders should be seriously considered in policies of introduction prevention.

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