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The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range?

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ABSTRACT

Aim The use of species distribution models (SDMs) to predict biological invasions is a rapidly developing area of ecology. However, most studies investigating SDMs typically ignore prediction errors and instead focus on regions where native distributions correctly predict invaded ranges. We investigated the ecological significance of prediction errors using reciprocal comparisons between the predicted invaded and native range of the red imported fire ant (*Solenopsis invicta*) (hereafter called the fire ant). We questioned whether fire ants occupy similar environments in their native and introduced range, how the environments that fire ants occupy in their introduced range changed through time relative to their native range, and where fire ant propagules are likely to have originated.

Location We developed models for South America and the conterminous United States (US) of America.

Methods We developed models using the Genetic Algorithm for Rule-set Prediction (GARP) and 12 environmental layers. Occurrence data from the native range in South America were used to predict the introduced range in the US and vice versa. Further, time-series data recording the invasion of fire ants in the US were used to predict the native range.

Results Native range occurrences under-predicted the invasive potential of fire ants, whereas occurrence data from the US over-predicted the southern boundary of the native range. Secondly, introduced fire ants initially established in environments similar to those in their native range, but subsequently invaded harsher environments. Time-series data suggest that fire ant propagules originated near the southern limit of their native range.

Conclusions Our findings suggest that fire ants from a peripheral native population established in an environment similar to their native environment, and then ultimately expanded into environments in which they are not found in their native range. We argue that reciprocal comparisons between predicted native and invaded ranges will facilitate a better understanding of the biogeography of invasive and native species and of the role of SDMs in predicting future distributions.

Keywords

Bioclimatic envelope, ecological niche models, evolution, future projections, geographical distribution, invasive, niche conservatism, *Solenopsis invicta*, species distribution models.

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INTRODUCTION

Invasive species threaten global biodiversity, but also represent unparalleled opportunities to explore ecological factors that

limit the distribution of species, and how and why those distributions change across space and time. In many ways this opportunity has not been fully realized, particularly in the context of species distribution models (SDMs). SDMs (also termed bioclimatic

envelopes or ecological niche models) are often used to predict the potential spread of invasive species by first relating the observed distribution of a species to environmental conditions in its native range and then projecting these relationships in space to predict the potential distribution of the species in an unoccupied region (e.g. Welk *et al.*, 2002). Most studies investigating this approach have focused on the prediction successes, i.e. regions where the native range correctly predicts the invaded range, and then consider regions in which ranges are predicted to expand (e.g. Peterson & Vieglais, 2001; Peterson *et al.*, 2003; Peterson, 2003). However, all SDM predictions have errors, which have largely been ignored. Some such errors may represent inadequacies in the algorithm or data used to perform modelling, and may hold little biological meaning (Fielding & Bell, 1997). Alternatively, and of greater potential interest to ecologists, errors may reflect genuine ecological differences between native and invaded ranges if they result from biological processes not included in models, such as interactions among species, dispersal, history, resource heterogeneity and evolution of environmental tolerances (Beerling *et al.*, 1995; Fielding & Bell, 1997; Peterson & Holt, 2003; Fitzpatrick & Weltzin, 2005; Holt *et al.*, 2005; Wiens & Graham, 2005).

Here we use a new method, reciprocal distribution modelling (RDM), to investigate the biological meaning and significance of prediction errors in modelling the distribution of invasive species (Fitzpatrick & Weltzin, 2005). RDMs are conceptually similar to SDMs, in that they assess the ability of the native range to predict the invaded range. However, RDMs also use distributional data from the *invaded* range to predict the *native* range, and evaluate the degree and spatial location of prediction errors. The spatial patterning of prediction errors relative to observed ranges can suggest non-climatic control of distributions. For example, Beerling *et al.* (1995) used models developed from the introduced European range of *Fallopia japonica* to predict its native Asian distribution. They found that the invaded range over-predicted the native range, and suggested that dispersal limitations and interspecific interactions explained the discrepancies between the observed and predicted native distribution.

In this study, we assess spatial and temporal patterns of prediction errors relative to the native and invaded distributions of the red imported fire ant (*Solenopsis invicta* Buren) (hereafter referred to as the fire ant), a noxious invader to the southeastern United States (US) of America (Tschinkel, 1993). Specifically, we use RDM and the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Noble, 1992; Stockwell & Peters, 1999) to address three questions. (1) Do fire ants occupy the same environments in their native and invaded range? (2) How did environments that characterized the occurrence of fire ants in the US change through time relative to the native range? (3) Can RDM be used to determine the likely origin of fire ant propagules from South America? We conclude that reciprocal comparisons between actual and predicted native and invaded distributions facilitate development of explanatory and mechanistic biological hypotheses for the factors that mediate species distributions.

METHODS

Modelling approach

SDMs are empirical models that relate the observed distribution of a species and environmental data to predict the potential distribution of the species (reviewed by Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Once developed from the native distribution, SDMs can be applied to another region to identify areas prone to invasion there (Peterson, 2003).

RDMs rely on this same basic approach, but differ in that they use models developed concurrently from separate and independent occurrence data sets, one from the native range and one from the invaded range, and then make reciprocal predictions of native and invaded ranges based on these models (Fitzpatrick & Weltzin, 2005). The RDM approach proceeds in four distinct steps. First, we model the native distribution based on native range occurrences. Secondly, we apply native range models to the invaded range and compare the predicted invaded range to the observed invaded range. Thirdly, we model the invaded distribution based on invaded range occurrences. Finally, we apply invaded range models to the native range and compare the predicted native distribution to the observed native distribution. This process produces four predicted distributions: two of the native range and two of the invaded range, from which we note the degree and spatial locations of prediction errors relative to observed and predicted native and invaded ranges. We assess model quality during the first and third steps, as described below.

Study species

We chose the fire ant as a model system because its present native and invaded distributions are relatively well known, its record of introduction and subsequent spread are well documented, and its life history is at least somewhat known in both its native and invaded range. The native range of the fire ant encompasses southern Brazil, Paraguay, Uruguay, Bolivia and north-eastern Argentina (Buren *et al.*, 1974; Pitts, 2002). Fire ants established in the US near Mobile, Alabama, in the 1930s (Callcott & Collins, 1996), and have since spread throughout the southeastern US and into Texas, New Mexico and California, and as far north as Maryland and Delaware. Fire ants have also recently invaded several Caribbean islands (Davis *et al.*, 2001).

Model inputs

Native and introduced distribution data sets consisted of presence data only. We collected 74 native range occurrences of fire ants within South America from primary literature (Allen *et al.*, 1974; Buren *et al.*, 1974; Pitts, 2002). For invaded range occurrence data, we used latitude–longitude centre points of only those US counties under ‘entire county quarantine’ by the US Department of Agriculture, Animal and Plant Health Inspection Service (APHIS, 2004), which constituted 741 counties in 2004. We obtained year of first infestation for these 741 quarantined counties from the National Agricultural Pest Information System

Table 1 Occurrence data sets used to develop reciprocal distribution models of fire ants

Dataset	Training/time period	Training/new points	Total points	Test data (extrinsic)	Division in GARP (%)	Test data (intrinsic)
Native range	—	—	74	37/37	70/30	26/11
Invaded range t_1	1930–1952	30	30	30/0	70/30	21/9
Invaded range t_2	1930–1959	173	203	102/101	50/50	51/51
Invaded range t_3	1930–1966	172	375	188/187	50/50	94/94
Invaded range t_4	1930–1979	184	559	280/279	50/50	180/140
Invaded range t_5	1930–2004	182	741	371/370	50/50	185/185

(Table 1; APHIS, 2004). Because we used centres of counties instead of actual locations of populations, we wanted to ensure to the greatest degree possible that our models did not include what may be temporary, or isolated, populations. Thus, by including full-quarantine counties in the US only, we excluded Caribbean islands and counties where fire ants have invaded, but may not be firmly established, such as locations in the western US (where counties tend to be large and environmentally heterogeneous). Further, developing models using full-quarantine counties only allowed us to demonstrate how the use of occurrence data from an invading population impacts upon the predictions of RDMs and to avoid potential biases of including absences that may result from active colonization rather than from environmental suitability. Environmental data consisted of 12 WorldClim data sets (Hijmans *et al.*, 2004) at 10-minute resolution, including elevation and 11 bioclimatic variables that summarize temperature and precipitation aspects of climate — variables typically used to develop SDMs (Table 2).

Reciprocal distribution modelling

We modelled distributions using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Noble, 1992; Stockwell & Peters, 1999). Applications of GARP to prediction of the potential distributions of invasive species have been described elsewhere (e.g. Peterson *et al.*, 2002; Peterson, 2003). In short, GARP uses an iterative process, and several individual modelling algorithms (e.g. logistic regression, bioclimatic rules), to develop, modify and test models describing the relationship between the presence of the species and environmental conditions. Training data (50% of the original occurrence data set, the remaining 50% were set aside as extrinsic tests of model quality) are divided by GARP, based on user specification, into intrinsic training and test data. GARP uses the training data and one of the individual algorithms to develop a rule predicting the distribution of the species. The rule is then modified and re-assessed for predictive accuracy. The change in predictive accuracy between iterations is

Variable	Abbreviation	Factor Loadings		
		PC-1	PC-2	PC-3
Elevation (m)	ELEV	0.005	0.031	0.915
Mean annual temperature (°C)	MAT	-0.907	0.300	-0.219
Mean diurnal temperature range* (°C)	MDTR	0.529	0.265	0.535
Isothermality†	ISO	-0.900	-0.075	0.333
Temperature seasonality ($\sigma \times 100$)	TSEAS	0.978	0.084	-0.111
Maximum temperature of warmest month (°C)	MXTWM	0.091	0.833	-0.359
Minimum temperature of coldest month (°C)	MTCM	-0.973	0.077	-0.153
Temperature annual range‡ (°C)	TAR	0.964	0.193	0.031
Annual precipitation (mm)	APR	-0.233	-0.907	-0.033
Precipitation of wettest month (mm)	PWM	-0.710	-0.537	0.023
Precipitation of driest month (mm)	PDM	0.509	-0.801	-0.148
Precipitation seasonality§	PSEAS	-0.742	0.527	0.189
Eigenvalue		6.12	2.94	1.50
Percentage variance		51.1	24.5	12.6
Cumulative percentage variance		51.1	75.6	88.2

*Mean monthly (max. temperature – min. temperature).

†Mean diurnal range/temperature annual range.

‡Max. temperature of warmest month – min. temperature of coldest month.

§Coefficient of variation.

Table 2 Environmental variables (including units, and abbreviations used in Fig. 3) used to develop predictions of potential distributions of fire ants, and principal components analysis (PCA) of environmental conditions associated with the presence of fire ants

used to determine whether the rule is incorporated into the model. The final model, a set of rules describing the distribution of the species, is selected after either 1000 iterations or when predictive accuracy converges between iterations. We selected GARP to develop models because the algorithm is well-established in the literature as a method to successfully predict distributions using presence-only data sets, and its predictions are considered more robust than similar approaches (Peterson & Cohoon, 1999; Stockwell & Peterson, 2002).

Native range modelling

We randomly assigned the 74 native range occurrences into 50/50 splits of extrinsic training and test data. To ensure that division of the data did not influence model quality, we repeated the randomization process 10 times. The 10 resulting training data sets contained a random sample of half of the 74 original occurrences. Within GARP, we specified that these training data be divided 70/30 into intrinsic training and test data.

We produced 100 models from each of the 10 training data sets, for a total of 1000 models. Because model development is stochastic, and resultant models vary in quality, we used a procedure described by Anderson *et al.* (2003) to select the best subset of models. From the 1000 models, we retained either all models with zero omission errors (i.e. false negatives) based on intrinsic test data, or, if there were less than 200 models with omission errors of zero, we selected the 200 models with lowest omission error rates. Using this subset, we calculated the median area predicted as present and selected 100 models closest to this median area. We then summed this best subset of 100 models to produce a final composite prediction ranging from zero (no models predict the presence of fire ants) to 100 (all models predict the presence of fire ants).

We evaluated models by comparing the proportional area predicted as occupied by fire ants against the number of extrinsic test points that would be occupied if fire ants were distributed randomly (χ^2 statistic) (Peterson & Shaw, 2003). Native range models were projected onto the invaded range and summed to produce a composite prediction of the potential invaded distribution of the fire ant relative to its known invaded range.

Invaded range modelling

We assigned the 741 invaded range occurrences to one of five groups based on year of first infestation in the US (Table 1). The first group (t_1) encompassed the first 20 years of fire ant invasion (i.e. 1930–52) and included 30 US counties, a minimum number of locations required for robust predictions in GARP (Stockwell & Peterson, 2002). We divided the remaining occurrences such that each successive group contained an equal number of newly invaded counties.

To ensure that our use of county centre points (as opposed to actual occurrences) in the invaded range did not influence model quality, we also constructed models using random points in each county. Models based on random points did not differ

qualitatively from models based on centre points; thus, we used centre points for all subsequent analyses.

To develop invaded range models from the five invaded range data sets, we employed a procedure similar to that used for native range models, with two modifications. First, the initial time series data set was too small to divide into extrinsic training and test data, so we used all 30 points for model development in GARP and did not evaluate these models using χ^2 tests. Secondly, the remaining four data sets were sufficiently large, so we specified GARP to divide training data sets into 50/50 (instead of 70/30) splits of intrinsic training and test data (Table 1). Otherwise, random partitioning of data sets, development and selection of best models, and model evaluation followed procedures described above. Invaded range models were projected onto South America and summed to produce a composite prediction of the native range of the fire ant relative to its known native range.

Environmental correlates with fire ant distributions

We used principal components analysis (PCA) on the correlation matrix (using NCSS; Hintze, 2001) to analyse patterns of fire ant distribution in relation to environmental data (listed in Table 2) for each occurrence point. Our PCA model included occurrence points from invaded range time period t_1 (30 points), invaded range time periods t_2 – t_5 pooled (711 points total), and the current native range (74 points).

RESULTS

Predictions based on native range occurrences

All 100 best native range models performed better than random expectation (χ^2 test, d.f. = 1, $P < 0.001$). Predicted distributions coincided with the extent of the native range in South America on the southern, western and northern boundaries, but extended considerably beyond the eastern boundary (Fig. 1a). Conversely, projections of native range models onto the invaded range in North America greatly under-predicted the actual extent of invasion (Fig. 1b). According to these models, peninsular Florida and the Pacific Northwest in the US, the Gulf Coast and Yucatan Peninsula in Mexico, and the Caribbean are most susceptible to invasion. Several models (< 25) also identified a narrow band of suitable environments along the Gulf Coast of the US, including where fire ants first established in southern Alabama.

Predictions based on invaded range occurrences

All the best invaded range models performed better than random expectation (χ^2 test, d.f. = 1, $P < 0.001$). Predicted distributions of the invaded range based on all 741 invaded counties overlapped the actual extent of invasion (Fig. 1c). Models predicted several areas beyond the extent of the current invaded range to be prone to invasion by fire ants as well, in particular the central valley of California, the Pacific North-west, and north of the current northern limit of the invaded range in the south-eastern

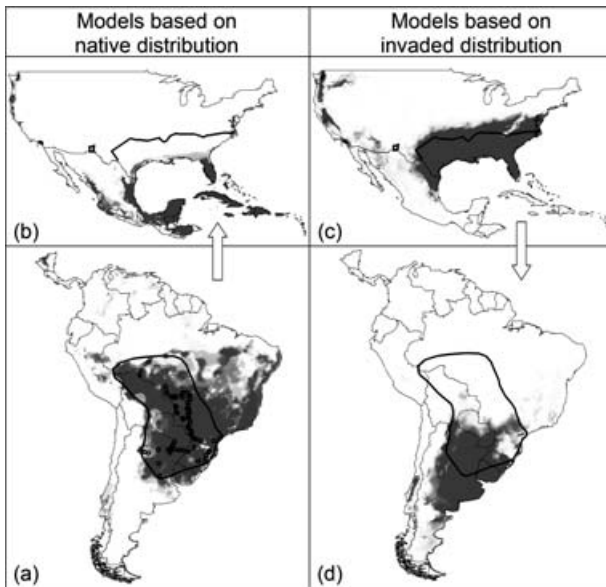


Figure 1 Potential distributions of the red imported fire ant. Native range models represent (a) the potential native, and (b) invaded distributions of the fire ant based on 74 known occurrences in South America (a, open circles). Invaded range models represent (c) the potential invaded, and (d) native range of the fire ant based on the centre points of 741 US counties (c, points not shown). Bold, solid lines indicate the approximate extent of the native (a, d) and invaded (b, c) range of the fire ant. Darker shading represents greater model agreement.

US. Over-prediction in these regions overlaps many US counties where fire ants have invaded, but that are not currently quarantined (APHIS, 2004). These findings are qualitatively similar to other attempts to predict fire ant distributions in North America, using both statistical (Sutherst & Maywald, 2005) and simulation (Killion & Grant, 1995; Korzukhin *et al.*, 2001) models. Invaded range models, when projected onto South America, predicted a distribution that overlapped only the southern half of the native range and extended several degrees of latitude (*c.* 1000 km) beyond the southernmost limit of the native range in Argentina (Fig. 1d).

When superimposed, predicted distributions of the native range developed using the five temporal data sets comprised of invaded US counties (Table 1; Fig. 2a) produced a bull's eye pattern (Fig. 2b). Models based on the first 30 invaded counties in the US predicted a limited and patchy distribution near the southernmost region of the native range. Each successive prediction (based on the temporally expanding distribution of fire ants in North America) grows radially from its predecessor, ultimately spreading equally north and south of the southern limit of the native range.

Comparison of predicted distributions

Native and invaded range occurrence data did not predict similar distributions in either North or South America. In South America, predicted distributions from native and invaded range models overlapped in the southern half of the native range only

and did not overlap in the northern half of the native range or regions in Argentina south of the native range (Fig. 1a,d). In North America, prediction distributions from both data sets overlapped in peninsular Florida, along the coast of the Gulf of Mexico, the Pacific Northwest, although they differed across large portions of the south-eastern and western US and the Caribbean (Fig. 1b,c).

Environmental correlates with fire ant distributions

The first three principle components accounted for 88.2% of the total variation in the data (Table 2). The first principle component (PC-1) was related to aspects of temperature, whereas PC-2 was related to precipitation and maximum temperature of the warmest month. PC-3 was related to elevation.

DISCUSSION

We report three novel findings related to the spatial patterning of prediction errors that would be largely indiscernible without reciprocal comparisons of predicted native and invaded distributions. First, fire ants occupy environments in their invaded range that they do not occupy in their native range. The environments that fire ants occupy in North America, but not in South America, tend to be colder and drier (Fig. 3) and characteristic of environments adjacent to, and south of, the southern border of their native range (Fig. 1). Second, comparisons of predicted distributions through time suggest that fire ants initially invaded environments in North America that were similar to those found within their native range, and subsequently spread into harsher environments outside their native range (Fig. 2). Finally, the extreme southern extent of the native range is most environmentally similar to US counties in which fire ants initially established, suggesting the southern region of the native range is a potential source of invading propagules. This result corroborates a similar prediction made by Mescher *et al.* (2003) based on genetic analyses. Together, our findings suggest a model in which fire ants from a peripheral native population established in an environment similar to their native environment, and then over time expanded into environments in which they are not found in their native range. We discuss our results below both in terms of their ecological interpretation and their broader implications for predicting future distributions using SDMs.

Native vs. invaded range environments

Fire ants in the US occupy colder, drier and more seasonal environments than in their native range (Fig. 3). Differences between the environments fire ants occupy in their native and invaded ranges are apparent as prediction errors in reciprocal comparisons (Figs 1 and 2b). Two broad hypotheses may explain these disparities between predicted and observed distributions of fire ants in the US. First, factors governing the southern boundary of the native range of the fire ant may not be present, or may not be limiting, in the invaded range. Secondly, and not mutually exclusive of the first hypothesis, environmental tolerances of the

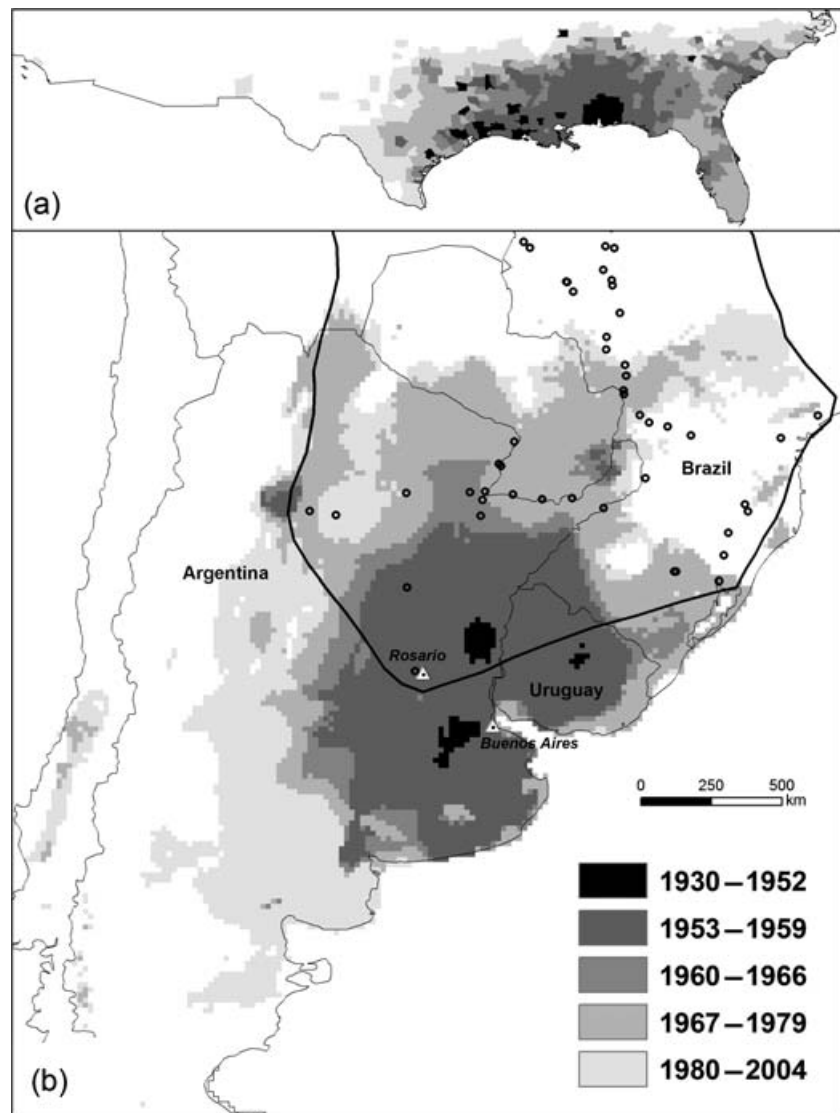


Figure 2 (a) Actual US counties invaded by fire ants, showing initial establishment in counties radiating from southern Alabama. (b) Predicted distributions of the fire ant in South America based on models from these time series data, relative to known occurrences (open circles) and the extent of the native range (bold line). Triangles indicate the port cities of Rosario and Buenos Aires, Argentina. Shading represents areas predicted by a majority (> 50) of the 100 best models.

fire ant may have changed post-invasion. In particular, a hypothesis that accounts for both of these possibilities is that genetic changes subsequent to introduction and release from natural enemies resulted in changes in the social structure of fire ants, which in turn promote their invasive success by allowing fire ants to form dense, ecologically destructive colonies (Tschinkel, 1998; Tsutsui & Suarez, 2003).

To our knowledge, no studies have explicitly investigated factors that limit the distribution of fire ants in both their native and invaded ranges. However, several lines of evidence suggest North and South American populations of fire ants demonstrate different life histories and experience different biotic environments, including (in North America): (1) higher rates of dispersal (Mescher *et al.*, 2003), (2) greater population densities, possibly resulting from enemy release (Porter *et al.*, 1997), (3) changes in social structure such that fire ants in the US form dense, polygynous colonies of unrelated queens free from density-limiting effects of territorial defence (Morel *et al.*, 1990; Porter & Savignano, 1990), (4) absence of infection by *Wolbachia*, a bacterium that can

reduce the fitness of its hosts (Shoemaker *et al.*, 2000), and (5) reduced competition stemming from anthropogenic disturbance and chemical eradication programmes that ultimately benefit fire ants while adversely affecting native North American ant species (Tschinkel, 1993; Zettler *et al.*, 2004).

Release from natural enemies is one of the most commonly invoked explanations for the proliferation of invasive populations (Colautti *et al.*, 2004), and the success of introduced fire ants has been attributed to enemy release (Porter *et al.*, 1997). Such release could allow fire ants to invade regions in which the combined mortality due to environmental and biotic factors would be too high to persist in the native range. Reduced biotic stresses stemming from the loss of natural enemies, coupled with increased dispersal rates (which could rescue peripheral populations), could reduce constraints on the distribution of introduced fire ants such that they can occupy a different set of environments in North America than those characteristic of their native range in South America.

Reduction of biotic stresses could also facilitate the initial establishment of propagules in non-optimal environments in

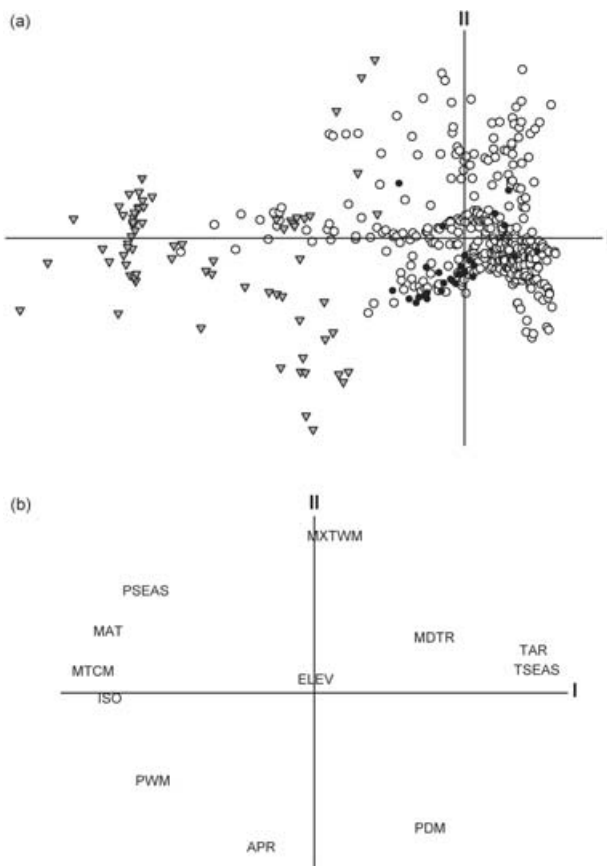


Figure 3 (a) PCA ordination of environmental variables associated with the presence of fire ants in their native South American range (triangles) and their invaded US range (circles). Closed circles represent the first 30 counties in which fire ants became established in the US between 1930 and 1952. Open circles represent US counties in which fire ants became established between 1953 and 2004; one-half of the open circles were excluded at random to reduce excessive detail. (b) Contribution of environmental variables to the distribution of points along each axis. Abbreviations of environmental variables and factor loadings for each principle component are given in Table 2.

North America. Less than 25% of distribution models based on native occurrences predicted fire ants to be present in the Mobile basin (Fig. 1b). In contrast, all models predicted fire ants to be present in peninsular Florida. However, fire ants did not occupy these potentially more favourable environments in Florida until later stages of the invasion (Fig. 2a). This suggests that if broad-scale environmental conditions alone controlled the establishment of fire ants in the US, and ignoring other factors potentially important to initial establishment, namely propagule pressure, then Florida was probably more susceptible than was Alabama as the primary point of initial establishment.

The expansion of invasive fire ants into environments in which they do not occur in their native range could result from changes in biotic interactions, but it could also be due to the evolution of life-history traits that facilitate persistence in novel environments. Rapid evolution of introduced species is widely reported (see Cox, 2004), and evolutionary changes in environmental toler-

ances of introduced fire ants could easily explain differences between environments occupied in the native and invaded range. Consistent with this hypothesis, and with our prediction that fire ants may have established in marginal environments, Holt *et al.* (2005) theorized that evolution of environmental tolerances is most likely if species are introduced into novel environments just outside their optimum environment.

Although there is no published evidence of evolution of environmental tolerances of fire ants *per se*, there is evidence of genetic changes subsequent to introduction coupled with changes in social structure that have influenced the success of fire ants as an invasive species (reviewed in Tsutsui & Suarez, 2003). Native and invasive fire ant colonies possess two social forms: colonies are either monogynous and contain a single queen, or colonies are polygynous and contain multiple queens. The polygynous colonies were not reported in the US until 20 years after the monogyne form was first detected, possibly stemming from multiple introductions (Tsutsui & Suarez, 2003). The appearance of the polygyne form in the US is significant because, unlike monogynous colonies, workers from polygynous colonies display reduced aggression towards individuals from other colonies (Morel *et al.*, 1990). Invasive polygynous colonies, free from density-limiting effects of territorial defence, attain greater densities of both workers and nest mounds than monogyne populations (Porter & Savignano, 1990). The ecological destructiveness of polygynous colonies and their ability to displace native ant species and previous invaders (including monogynous colonies) are correspondingly greater (Porter & Savignano, 1990). Thus, polygyny may allow fire ants to invade harsher environments by reducing both biotic resistance and extinction risk through increased abundance.

Hybridization could also facilitate persistence in novel environments. In the US, the fire ant hybridizes with another pest ant species, *Solenopsis richteri*, the black imported fire ant (Shoemaker *et al.*, 1996). Hybridization might lead to introgression of genes favouring range expansion into colder and drier environments. In South America, the native range of *S. richteri* overlaps the southern portion of the native range of *S. invicta* and extends southward into colder and drier environments in Argentina (Pitts, 2002; Ross & Shoemaker, 2005), but hybridization does not appear to occur in the native range (Ross & Shoemaker, 2005). Finally, an additional genetic/evolutionary hypothesis is that, in the native range, local adaptation to conditions at the edge of the range (where the invasive propagules appear to have originated, see below) are not possible because of gene flow with the centre of the range where less extreme conditions predominate.

Source of founding propagules

Based on reciprocal comparisons we identify the extreme southern extent of the native range as being most environmentally similar to counties in the US initially invaded by fire ants (darkest shading in Fig. 2b). If greater environmental similarity between source and recipient locations increases the likelihood of successful establishment, then the southern portion of the native range is the most likely source of invading propagules.

Several other lines of evidence also support the suggestion that the southern portion of the native range represents the source of propagules. First, preliminary genetic analyses of native and invasive fire ant populations also suggest that the most likely source of individuals founding the US population is the southern half of the native range, and north-eastern Argentina in particular (Mescher *et al.*, 2003). Secondly, Ahrens *et al.* (2005) reported a sharp genetic discontinuity in the native distribution of fire ants along the border between Argentina and Brazil. In this region, a 2500 km-long geographical barrier to gene flow (the Mesopotamia wetlands) divides the distribution of fire ants into two evolutionary independent groups, one in the south-western portion of the range and the other in the north-eastern portion (Ahrens *et al.*, 2005). Environments characteristic of the counties first invaded by fire ants occur primarily to the west of this division. Finally, historical patterns of commerce provide circumstantial evidence that propagules are likely to have originated from the southern portion of the native range. When fire ants were first discovered in the US, the port in Mobile, Alabama, was receiving cargo from eastern South America (Buhs, 2004). Ships originating in South America often used soil as ballast, which was unloaded in Mobile when American goods were loaded for transport back to South America (Buhs, 2004). Rosario and Buenos Aires, two massive port cities in Argentina, occur within 150 km of the regions we identified as most environmentally similar to the areas where fire ants first established in the US (Fig. 2b). Taken together, these findings suggest that populations of fire ants west of the Mesopotamia wetlands in north-eastern Argentina, near the port cities of Rosario and Buenos Aires, are the most likely source of fire ants introduced to the US. Evolutionary biologists searching for the founding populations of fire ants should focus their attention on this region.

Caveats

As stated above, prediction errors can result from both a failure to account for biotic processes (the interesting errors) and/or from inadequacies in the algorithm or data (the problematic errors). Of potentially greatest concern to the use of RDMs, in terms of inadequacies in the algorithm or data, are incomplete distribution data. Apparent prediction errors (e.g. over-prediction of the native range) could represent environments where the species is present but has yet to be detected. Incomplete distribution data, however, seem an unlikely explanation for the prediction errors observed in our analysis because *S. invicta* apparently has yet to be collected south of Rosario, Argentina, despite surveys in this region (Pitts, 2002; Ross & Shoemaker, 2005). Instead, other species of fire ants occur south of Rosario, such as *S. richteri* (Pitts, 2002; Ross & Shoemaker, 2005).

Of secondary concern to the application of RDMs is that many invasive species may still be expanding their distribution, in which case the introduced range may be more immediately constrained by dispersal and time than by environmental factors (Welk, 2004). However, invasive species often spread rapidly. Therefore, although an introduced species may be actively spreading in some parts of its range, its distribution

may be limited by environmental tolerances in other areas, or the species may have already colonized novel environments. If this were the case, we would expect RDMs to over-predict portions of the introduced range that are suitable, but not yet invaded, and under-predict environments in the native range that are not currently invaded in the introduced range. This is precisely the pattern observed in our study. Our analysis suggests the introduced range of the fire ant could expand to include tropical Mexico and the Caribbean (as over-predicted by our models), which have environments similar to the northern-most portion of the native range (as under-predicted by our models). Consistent with our prediction, fire ants recently invaded several Caribbean islands (Davis *et al.*, 2001). However, the southward expansion of fire ants into Mexico may be biologically hindered given the gradient of increasing ant diversity with latitude (Kaspari *et al.*, 2003).

Implications for predicting future distributions

The projection of SDMs in space or time, either to predict biological invasions or the impacts of climate change on biodiversity, assumes: (1) climatic tolerances of the species are the primary determinants of its current distribution (as opposed to ecological factors, notably biotic interactions and dispersal limitation); and (2) climatic tolerances of the species are conserved such that the species will occupy similar environments in new biogeographical settings. Debate concerning the validity of this latter assumption, often referred to as 'niche conservatism' (reviewed in Wiens & Graham, 2005), has transpired in the recent literature. Our results suggest that novel biotic interactions and evolutionary change may invalidate the assumption of niche conservatism. That said, our models successfully predicted the initial stages of the invasion of fire ants into the US. Thus, although SDMs may predict regions where invaders are most likely to establish, they may be ineffective at predicting subsequent spread in some cases. Given the increasing application of SDMs, and their potential to (mis)inform conservation, it is important to investigate further the precepts of this approach and to integrate ecological principles more fully with SDMs. Our study demonstrates that reciprocal comparisons of the native and invaded ranges of invasive species can serve as powerful tests of the underlying assumptions of SDMs, and of niche conservatism in particular. We suggest that more studies incorporating reciprocal comparisons, and a greater focus on prediction errors, are required and should include additional modelling techniques, more invasive species and different regions of the globe. Such studies may lead to a better understanding of biological invasions, niche conservatism and the role of SDMs in predicting future distributions (Fitzpatrick & Weltzin, 2005; Wiens & Graham, 2005).

CONCLUSIONS

Our analysis allowed us to make four conclusions about the distribution of fire ants. First, we identified environments occupied in the invaded range but not in the native range. Secondly, we identified how the environmental conditions occupied by

fire ants in their invaded range have changed (non-randomly) through time relative to their native range. Thirdly, we identified a potential origin of source propagules. Finally, we identified regions of the invaded range into which fire ants may spread based on environmental tolerances. Although these four findings could ultimately be best further informed by field studies, they were detected using available occurrence data sets only. We propose that these types of analyses can be performed — and that consequent biogeographical hypotheses can be developed — for other species for which we know the native and invaded ranges well. Rather than focusing on prediction successes, we argue that reciprocal comparisons between predicted native and invaded ranges, coupled with careful scrutiny of prediction errors, will facilitate a better understanding of the biogeography of invasive and native species than was previously possible.

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