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PAPER



Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*

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ABSTRACT

Aim In response to a recent paper suggesting the failure of ecological niche models to predict between native and introduced distributional areas of fire ants (*Solenopsis invicta*), we sought to assess methodological causes of this failure.

Location Ecological niche models were developed on the species' native distributional area in South America, and projected globally.

Methods We developed ecological niche models based on six different environmental data sets, and compared their respective abilities to anticipate the North American invasive distributional area of the species.

Results We show that models based on the 'bioclimatic variables' of the WorldClim data set indeed fail to predict the full invasive potential of the species, but that models based on four other data sets could predict this potential correctly.

Main conclusions The difference in predictive abilities appears to centre on the complexity of the environmental variables involved. These results emphasize important influences of environmental data sets on the generality and ability of ecological niche models to anticipate novel phenomena, and offer a simpler explanation for the lack of predictive ability among native and invaded distributional areas than that of niche shifts.

Keywords

Climatic data, data sources, ecological niche modelling, fire ant, invasive species, niche shifts.

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INTRODUCTION

The emerging field of ecological niche modelling (ENM) has seen an impressive swell of attention, including applications to diverse biodiversity phenomena (Sánchez-Cordero & Martínez-Meyer, 2000; Peterson *et al.*, 2004; Thomas *et al.*, 2004; Araújo *et al.*, 2005; Thuiller *et al.*, 2005). With so much use of the methodology, numerous studies have now addressed methodological details as well – underlying theory (Guisan & Zimmermann, 2000; Soberón & Peterson, 2005; Araújo & Guisan, 2006), algorithm choice (Elith *et al.*, 2006), model evaluation techniques (Pearson *et al.*, 2006), occurrence data sample size (Stockwell & Peterson, 2002), environmental data density (Peterson & Cohoon, 1999) and other factors (Guisan, 2007a,b). Such critical examination will eventually lead the field to a more critical methodology, one that is well founded on the known behaviour of tested and reliable approaches.

An issue that has seen relatively little attention, however, is that of implications of different environmental data sets for development of ENMs. In particular, the possibility of development of general, predictive models that are able to extrapolate across space or time to predict biodiversity phenomena on novel landscapes may be heavily contingent on the appropriate choice of environmental data sources. In this paper, stimulated by a recent analysis (Fitzpatrick & Weltzin, 2005; Fitzpatrick *et al.*, 2007), we analysed a well-documented species' invasion – invasion by fire ants (*Solenopsis invicta*) from their native distributional area in South America into the southern United States – as well as the invasive potential of a non-invasive related species (*Solenopsis richteri*). We compared predictions based on six environmental data sets, and demonstrate clear differences in model generality when models are based on different environmental data sets. We emphasize that our purpose is primarily to clarify the reasons behind the arguable niche differences pointed out by previous authors (Fitzpatrick & Weltzin,

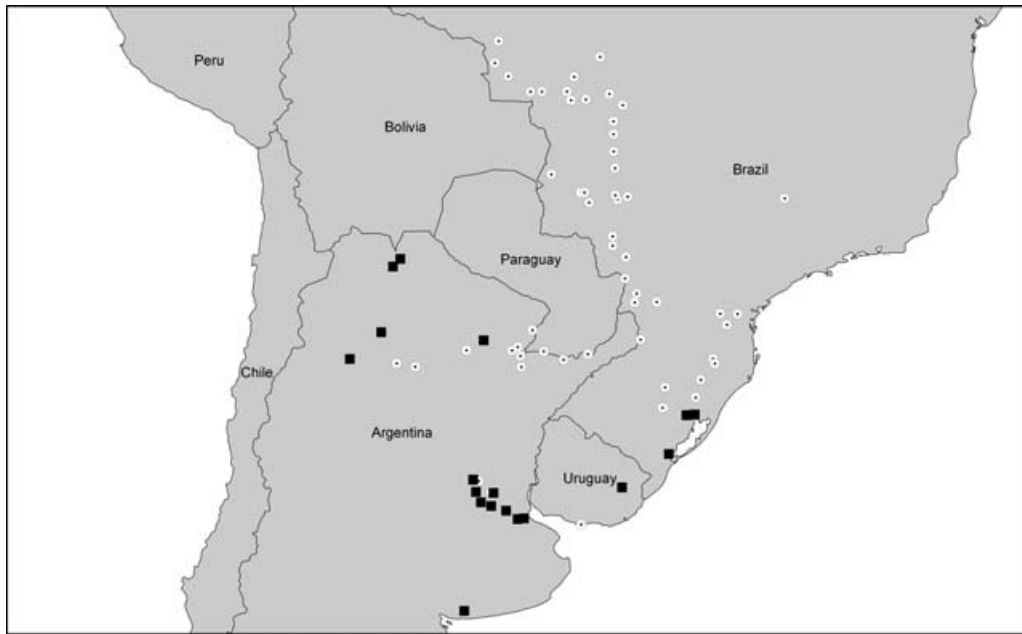


Figure 1 Map of occurrence data on native distributions in South America of *Solenopsis invicta* (dotted circles) and *S. richteri* (black squares).

2005; Fitzpatrick *et al.*, 2007), rather than to develop a definitive ecological and geographical profile of fire ants.

METHODS

Input data sets

We assembled occurrence points from the native distributions of *S. invicta* and *S. richteri* (Fig. 1), based on a compilation provided in a recent thesis (Pitts, 2002) and on locality data associated with museum specimens (see Acknowledgements). From these sources, we extracted names of the reported localities and proceeded to georeference them using an electronic gazetteer (Rand McNally, 1998) based on country, state/province and locality provided; when offsets were provided (e.g. Route 20, 60 km north of Posse), we measured distances along the road in the indicated direction to identify the exact locality. In all, we had available 61 *S. invicta* and 19 *S. richteri* unique localities for this analysis, which meets the sample size requirements identified in previous studies of the niche modelling algorithms employed herein (Stockwell & Peterson, 2002), at least in the case of *S. invicta* (*S. richteri* is included for the sake of comparison only).

We prepared six environmental data sets for comparison (Fig. 2) as follows: (1) for *data sets 1 and 2* we used the WorldClim data sets (Hijmans *et al.*, 2005) at 0.0416° and 0.167° spatial resolution, respectively (hereafter 'WC1' and 'WC2'), including the following 'bioclimatic' variables provided in the WorldClim data archive: mean annual temperature, mean diurnal temperature range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, annual mean precipitation, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality, the same as used in the pre-

vious analyses (Fitzpatrick *et al.*, 2007); (2) for *data set 3* we used data from the Intergovernmental Panel on Climate Change (IPCC) (IPCC, 2001), including the following variables: annual mean temperature, diurnal temperature range, frost-free days, annual mean precipitation, solar radiation, annual mean monthly minimum temperature, annual mean monthly maximum temperature, vapour pressure and wet days; native resolution of these data was 0.5°, but they were resampled artificially (i.e. the same grid values, finer resolution) to 0.05° resolution for analysis; (3) for *data set 4* an additional climate-based data set was drawn from the Center for Climate Research (CCR, University of Delaware) data set (Feddema, 2006), including the following variables: annual mean temperature and precipitation, actual and potential evapotranspiration, moisture deficit and surplus, soil moisture and minimum and maximum temperatures; these data, originally at 0.5°, were resampled to 0.05° for analysis; (4) for *data set 5* we used 12 monthly surface reflectance values drawn from the normalized difference vegetation index (NDVI), as measured by the Advanced Very High Resolution Radiometer (AVHRR) satellite (Tucker, 1979); these data sets were used at their native resolution of 0.08°; (5) for *data set 6* we used a subset of the data layers of WC2 (annual mean precipitation, annual mean temperature, minimum temperature of coldest month, maximum temperature of the warmest month) chosen to match the simpler data layers in data set 3 with the finer spatial resolution of the WorldClim data.

In the latter four data sets we also included variables summarizing topographic characteristics, including elevation, slope, aspect and compound topographic index (USGS, 2001) with a native resolution of 0.01° and resampled to the corresponding resolution for analysis depending on the environmental-climatic data. To avoid problems with overfitting models in spaces that are too highly dimensional, with IPCC data, CCR data and NDVI data, we chose a subset of coverages for analysis based on

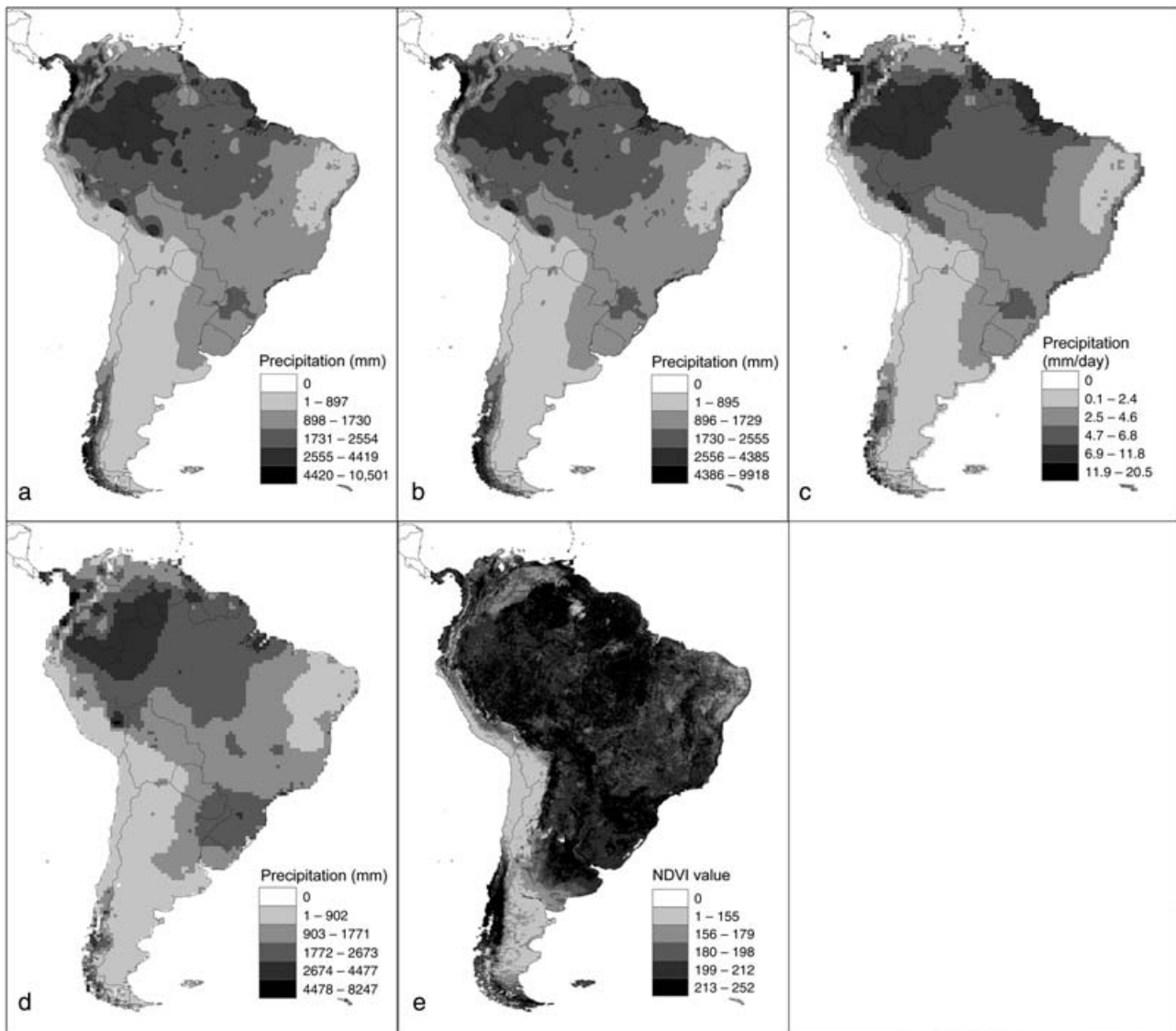


Figure 2 Examples of raster GIS data layers from each of the environmental data sets tested in this study, including annual mean precipitation for the four climate data sets and a monthly composite normalized difference vegetation index (NDVI) image for the remotely sensed data set. (a) WC1, (b) WC2, (c) IPCC, (d) CCR, (e) NDVI (see text for explanation). Note that the 6th data set analysed here, a coarser-resolution version of WC2, is equivalent to WC2 when viewed at this resolution.

a jackknife manipulation that explores which coverages are most informative (Peterson & Cohoon, 1999).

Ecological niche modelling

Our approach to ENM is based on the idea of ecological niches defined as the set of conditions under which a species is able to maintain populations without immigration (Grinnell, 1917, 1924). We used the genetic algorithm for rule-set prediction (GARP) (Stockwell & Peters, 1999) for ENM development. GARP uses an evolutionary computing genetic algorithm to search for non-random associations between environmental variables and known occurrences of species, as contrasted with environmental characteristics across the overall study area. Although comparative tests of ability to reconstruct the actual

distributions of species have indicated relatively poor performance by GARP (Elith *et al.*, 2006), the method has seen extensive testing and exploration for the challenge of reconstructing species potential distributions, such as in applications to invasive species (Peterson *et al.*, 2003, Peterson & Robins, 2003, Iguchi *et al.*, 2004). Nonetheless, we emphasize that GARP is but one methodological option (we obtained parallel results in preliminary experiments using Maxent; Phillips *et al.*, 2006), and is not the focus of this paper – rather, we use this technique to illustrate the effects of different environmental data sets on model quality.

Within the functioning of the GARP program, available occurrence points are resampled (with replacement) from the available occurrence data to create a population of 1250 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 internal testing (for evaluating model quality) data sets.

GARP models consist of sets of conditional rules developed through an iterative process of rule selection, evaluation, testing and incorporation or rejection (all within the program's processing, and not subject to user options). First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules, etc.), and applied to the training data set. Then a rule is developed and evolved by a number of means mimicking DNA evolution (point mutations, deletions, crossing over, etc.) to maximize predictive accuracy. Rule accuracy is evaluated via the testing data based on a significance parameter equal to 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 (i.e. did accuracy increase or decrease?). The algorithm runs either for 1000 iterations or until the addition of new rules has no effect on predictive accuracy ('convergence'; most models converge at 100–120 iterations, so the maximum iteration parameter is never reached in practice). The final rule-set, or ecological niche model, is then projected onto digital maps to identify a potential geographical distribution, either on the native distribution or worldwide.

Spatial predictions of presence and absence can include two types of error: omission (predicted absence in areas of actual presence) and commission (predicted presence in areas of actual absence) (Fielding & Bell, 1997). Because GARP is a random-walk procedure, it does not produce unique solutions; consequently, we followed recently published best-practice approaches to identify an optimal subset of resulting replicate models (Anderson *et al.*, 2003). In particular, for each species, we developed 100 replicate models; of these models, we retained the 20 with lowest omission error. Then, we retained the 10 models with intermediate commission error (i.e. we discarded the 10 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 in the form of grids with values ranging from 0 (all models agree in predicting absence) to 10 (all models agree in predicting potential presence).

Because we had a relatively small number of occurrence points for the two ant species, we did not attempt a validation of model predictions on the species' native range. Rather, for *S. invicta*, we compared the projection of the models across North America to its distributional limits as an invasive in North America (APHIS, 2004), and used the coincidence of the two as a measure of model quality. Our 'test' of model predictions was qualitative, but the failure of models to anticipate the full northward extent of the species' invasion was taken as an indication of poor generalization.

RESULTS

The native-range predictions for *S. invicta* based on environmental data sets 1–5 varied somewhat in their characterization of the species' native distribution (Fig. 3). WC1 and WC2 were similar

in their predictions, and can be characterized in general as identifying regions of uniform high predicted suitability, and to some degree reflected likely interpolation effects such as broad and smooth isoclines in the predictions. CCR predictions were very narrow and well defined, whereas IPCC predictions were broadest, showing blocky pixellation from the initially coarse resolution of the data sets. Finally, NDVI predictions were quite broad geographically (i.e. extending considerably farther northward than the other models), but were finely resolved and provided fine detail within the geographical distribution of the species.

Projections of the native-range *S. invicta* models to North America showed interesting differences (Fig. 4). The two WorldClim-based models failed to anticipate the ability of this species to extend northward out of peninsular Florida. The other three models largely succeeded in anticipating the geographic potential of the species as a North American invasive species. Projecting these models globally, the picture of global invasive potential of the species was fairly consistent, except that the two WorldClim-based predictions failed to predict potential distributional areas in Central Africa and Southeast Asia, although they did predict a broader distributional potential in Australia. Interestingly, models based on data set 6 (the extraction from the WorldClim data designed to match the IPCC data layers to every extent possible) performed similarly to the IPCC and CCR data sets and anticipated the full distributional potential of the species in North America.

Models for *S. richteri* were similar in the differences that they demonstrated among environmental data sets (Fig. 5). This species appears to have a somewhat more temperate ecological niche than *S. invicta*. The global projection of these models suggests that this species could have broader potential in temperate regions such as East Asia, South Africa and eastern North America.

DISCUSSION

In this paper we have developed preliminary ecological niche models of the potential ecological and geographical distribution of two species of fire ants. Although the models are intriguing, we hasten to point out that they are unlikely to be definitive, and could certainly be improved upon. In particular, addition of non-climatic data sets, such as characteristics of soils, landscape configuration and land use/land cover would likely refine our predictions considerably (Coudun *et al.*, 2006).

Environmental data sets

This study, more than anything, aimed to compare implications of different environmental data sets in developing general, predictive and extrapolative ecological niche models. In particular we took advantage of the careful documentation of the invasion of North America by *S. invicta* – the species invaded rapidly, and appears now to be reaching a range limit as the rate of spread has slowed considerably (APHIS, 2004). As such, for this species, we have at least an approximation of the 'truth' – the limits of the species' native and invaded distributions, each on a different continent.

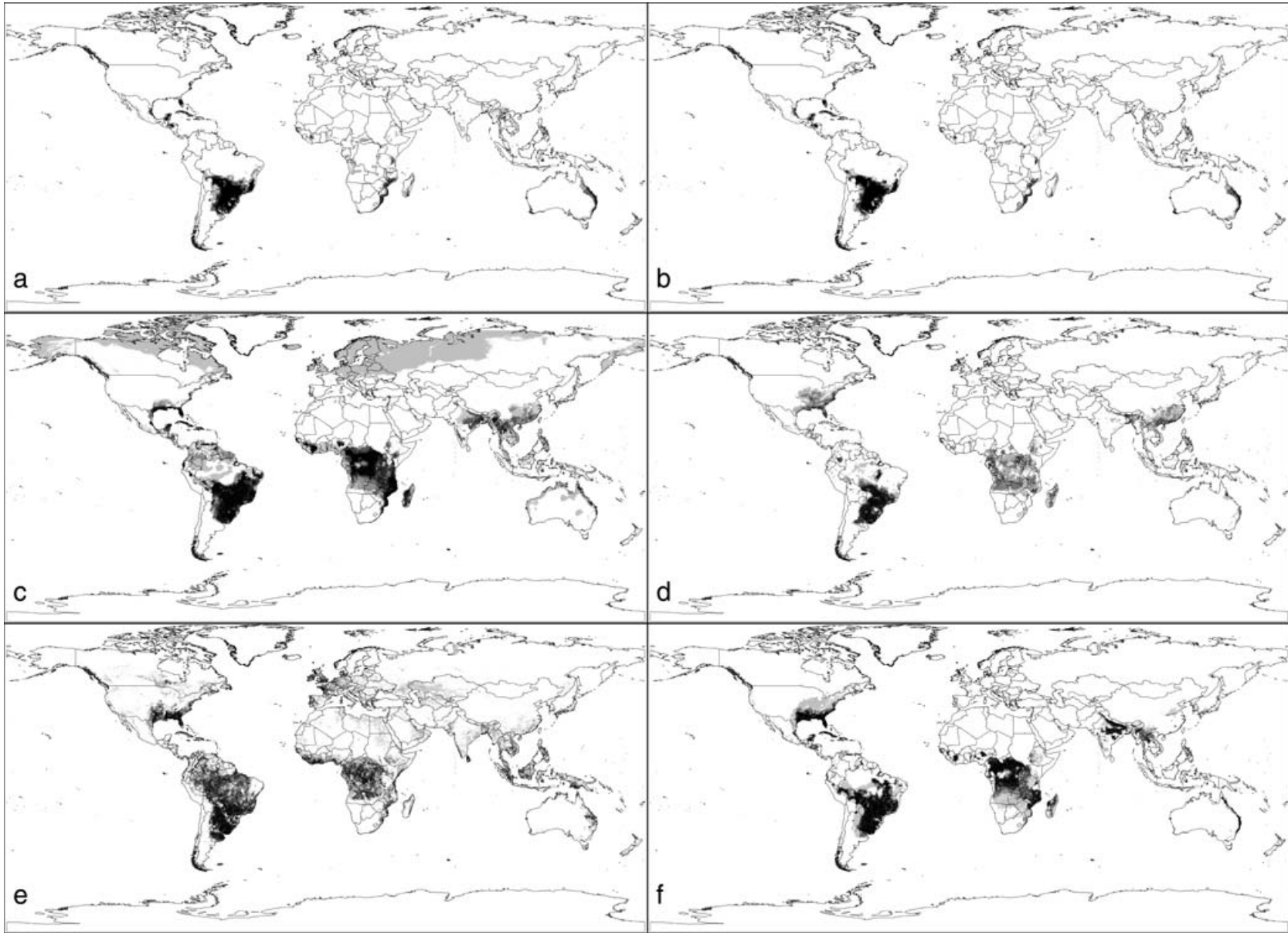


Figure 3 Map of predicted global potential distributions of *S. invicta* based on six different environmental data sets: (a) WC1, (b) WC2, (c) IPCC, (d) CCR, (e) NDVI and (f) reduced WC2 (see text for explanation). Model agreement in the prediction of presence versus absence is shown as a ramp from white (all models predict absence) to black (all models predict presence).

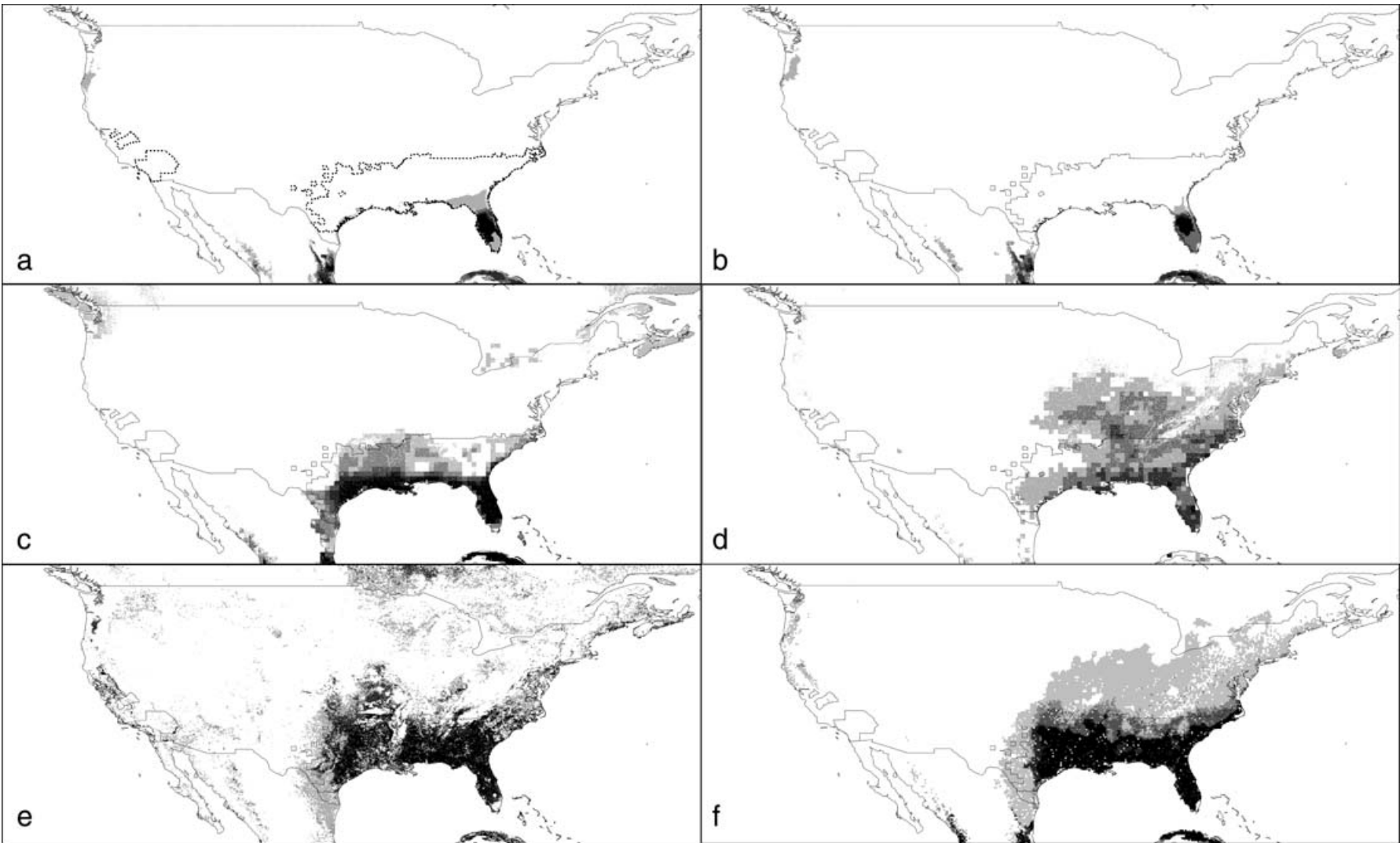


Figure 4 Map of predicted potential distributions of *S. invicta* in North America based on six different environmental data sets: (a) WC1, (b) WC2, (c) IPCC, (d) CCR, (e) NDVI and (f) reduced WC2 (see text for explanation). Model agreement in the prediction of presence versus absence is shown as a ramp from white (all models predict absence) to black (all models predict presence). The dotted line in panel (a) indicates the approximate present northern limit of the species' distribution as an invasive species (APHIS, 2004).

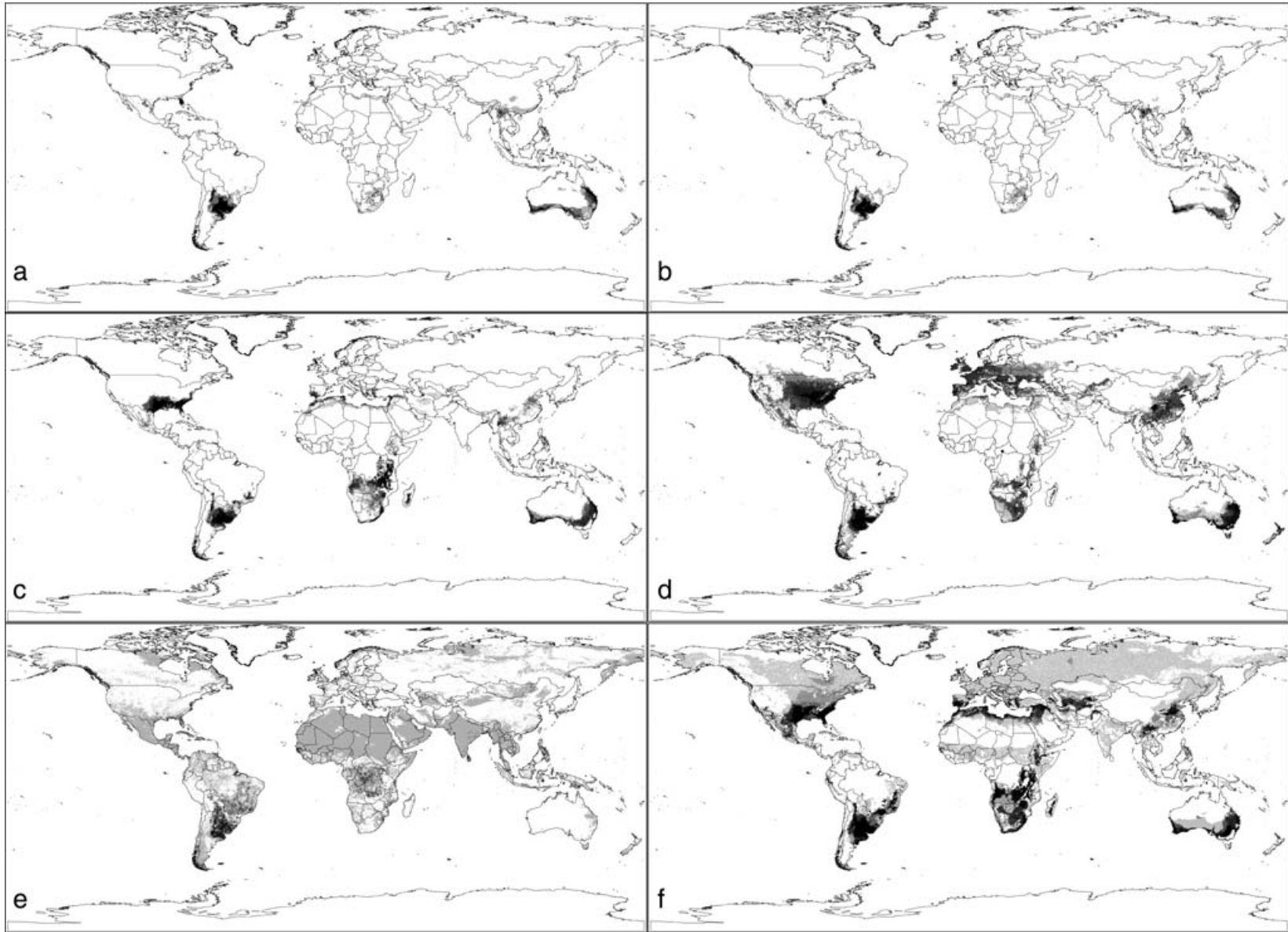


Figure 5 Map of predicted global potential distributions of *S. richteri* based on six different environmental data sets: (a) WC1, (b) WC2, (c) IPCC, (d) CCR, (e) NDVI and (f) reduced WC2 (see text for explanation). Model agreement in prediction of presence versus absence is shown as a ramp from white (all models predict absence) to black (all models predict presence).

On native distributional areas, predictions of models based on different environmental data sets were fairly similar, ranging subtly from broad and entire (IPCC), to narrow and defined (WC1, WC2), to somewhat overly extensive but with much detail within distributional areas (NDVI). Projections to North America, however, revealed differences – the two spatial resolutions used for the bioclimatic variable set of the WorldClim data set both underestimated the species' invasive potential considerably. Although the predictions of the NDVI and CCR models overestimated the species' distribution somewhat, this discrepancy may reflect the last details still to be filled in the North American invasion by the species. These differences strongly suggest that some environmental data sets may be less useful in global projections of invasive potential, although, of course, further corroboration and testing of these results will be necessary.

Why might such differences between environmental data sets exist? This question is not easy to answer – and certainly the details of climate modelling and interpolation are beyond our expertise. In this analysis, we controlled the dimensionality of environmental spaces used to characterize ecological niches (i.e. we used roughly the same numbers of variables in each analysis), yet the WC1 and WC2 WorldClim data sets showed clear differences in both the potential for and pattern of extrapolation to other regions. We can contemplate the differences in how different climate data sets are constructed – some via interpolation of information among climate stations, versus others extracted from global climate models, or potentially the construction of the 'bioclimatic' variables, versus more general and simple annual mean variables in the other data sets. Interestingly, WorldClim variables chosen to mimic the IPCC data dimensions (data set 6) performed much better, and much more in line with the IPCC, CCR and AVHRR data sets – this result suggests that the complex composite variables that make up the bioclimatic variables of the WorldClim data set may be responsible for the failure of WC1 and WC2 in anticipating the invasive potential of the species. In any case, the *biological* explanations for the non-predictivity between distributional areas suggested previously (Fitzpatrick *et al.*, 2007) (and, in fact, in other recent contributions of the same nature; Broennimann *et al.*, 2007) do not appear necessary – rather, methodological considerations suggest that the choice of environmental data sets may be responsible for the lack of correspondence. Nonetheless, our point in this paper is to provide the impetus for opening discussion of the distinct behaviours of models based on different environmental data sources – the results of this study clearly indicate that such a discussion will prove necessary for the further development of this field.

Fire ants

The examples examined herein to illustrate differences between environmental data sets are two ants of considerable actual (*S. invicta*) and potential (*S. richteri*) economic importance. Indeed, the United States, Australia and other countries have large-scale control programmes directed at *S. invicta* that cost immense sums of money and resources annually. As such, a

detailed understanding of the invasive potential of these species is of considerable interest – several previous studies have addressed these questions as well (Stoker *et al.*, 1994; Killion & Grant, 1995; Korzukhin *et al.*, 2001; Morrison *et al.*, 2004; Fitzpatrick & Weltzin, 2005; Sutherst & Maywald, 2005; Fitzpatrick *et al.*, 2007) – and given the availability of detailed information on both its native and its invaded ranges, this species is fast becoming a touchstone for such analyses.

The global potential distribution of *S. invicta* is interesting, in that the species sees broad possibilities for expansion. The models correctly predicted known areas of invasion in Hawaii, Australia and eastern North America, and suggest additional areas of potential invasion, for example in Africa. Interestingly, however, in the light of recent large-scale movements of military equipment from infested areas of North America to the Middle East (Iraq and Afghanistan), only the NDVI projections indicated any distributional potential in the region for the species, and that at a relatively low level.

Solenopsis richteri is not as yet an invasive species, but its close similarity in biology and natural history to *S. invicta* suggested initially that it might also have the potential to become an aggressive invader as well. Regions likely to be vulnerable to invasion by this species include southern Europe, East Africa, East Asia and eastern North America – at least on the basis of coarse-resolution climatic and landscape variables such as those used in the development of the models presented herein. As such, even in areas already infested by *S. invicta*, care should be taken with movements of materials from this species' native range in South America.

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REFERENCES

- Anderson, R.P., Lew, D. & Peterson, A.T. (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*, **162**, 211–232.
- APHIS (2004) *PestTracker: a public website of the NAPIS/CAPS database*. <http://www.ceris.purdue.edu/napis>.
- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Araújo, M.B., Thuiller, W., Williams, P.H. & Reginster, I. (2005) Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography*, **14**, 17–30.
- Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

- Coudun, C., Gégout, J.C., Piedallu, C. & Rameau, J.C. (2006) Soil nutritional factors improve plant species distribution models: an illustration with *Acer campestre* (L.) in France. *Journal of Biogeography*, **33**, 1750–1763.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S.E., Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Feddema, J.J. (2006) A revised Thornthwaite type global climate classification. *Physical Geography*, **26**, 442–446.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Fitzpatrick, M. C. & Weltzin, J. F. (2005) Ecological niche models and the geography of biological invasions: a review and a novel application. *Invasive plants: ecological and agricultural aspects* (ed. by S. Inderjit), pp. 45–60. Birkhäuser Verlag, Basel.
- Fitzpatrick, M.C., Weltzin, J.F., Sanders, N.J. & Dunn, R.R. (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Global Ecology and Biogeography*, **16**, 24–33.
- Grinnell, J. (1917) Field tests of theories concerning distributional control. *The American Naturalist*, **51**, 115–128.
- Grinnell, J. (1924) Geography and evolution. *Ecology*, **5**, 225–229.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Guisan, A., Zimmermann, N.E., Elith, J., Graham, C.H., Phillips, S. & Peterson, A.T. (2007a) What matters for predicting spatial distributions of trees: techniques, data, or species' characteristics? *Ecological Monographs*, in press.
- Guisan, A., Graham, C.H., Elith, J., Huettmann, F. & the NCEAS Species Distribution Modelling Group (2007b) Sensitivity of predictive species distribution models to change in grain size. *Diversity and Distributions*, **13**, 332–340.
- Hijmans, R.J., Cameron, S. & Parra, J. (2005) *WorldClim, version 1.3*. University of California, Berkeley (<http://biogeo.berkeley.edu/worldclim/worldclim.htm>).
- Iguchi, K., Matsuura, K., McNyset, K., Peterson, A.T., Scachetti-Pereira, R., Powers, K.A., Vieglais, D.A., Wiley, E.O. & Yodo, T. (2004) Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Transactions of the American Fisheries Society*, **133**, 845–854.
- IPCC (2001) *Climate data archive*. Intergovernmental Panel on Climate Change, Geneva (http://ipcc-ddc.cru.uea.ac.uk/cru_data/examine/HadCM2_info.html).
- Killion, M.J. & Grant, W.E. (1995) A colony-growth model for the imported fire ant: potential geographic range of an invading species. *Ecological Modelling*, **77**, 73–84.
- Korzukhin, M.D., Porter, S.D., Thompson, L.C. & Wiley, S. (2001) Modeling temperature-dependent range limits for the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the United States. *Environmental Entomology*, **30**, 645–655.
- Morrison, L.W., Porter, S.D., Daniels, E. & Korzukhin, M.D. (2004) Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. *Biological Invasions*, **6**, 183–191.
- Pearson, R.G., Raxworthy, C., Nakamura, M. & Peterson, A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.
- Peterson, A.T. & Cohoon, K.C. (1999) Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modelling*, **117**, 159–164.
- Peterson, A.T. & Robins, C.R. (2003) Using ecological-niche modeling to predict barred owl invasions with implications for spotted owl conservation. *Conservation Biology*, **17**, 1161–1165.
- Peterson, A.T., Papeş, M. & Kluza, D.A. (2003) Predicting the potential invasive distributions of four alien plant species in North America. *Weed Science*, **51**, 863–868.
- Peterson, A.T., Bauer, J.T. & Mills, J.N. (2004) Ecological and geographic distribution of filovirus disease. *Emerging Infectious Diseases*, **10**, 40–47.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Pitts, J.P. (2002) *A cladistic analysis of the Solenopsis saevissima species-group (Hymenoptera: Formicidae)*. PhD dissertation, University of Georgia.
- Rand McNally (1998) *Rand McNally new millennium world atlas deluxe*. Rand McNally & Co., New York.
- Sánchez-Cordero, V. & Martínez-Meyer, E. (2000) Museum specimen data predict crop damage by tropical rodents. *Proceedings of the National Academy of Sciences USA*, **97**, 7074–7077.
- Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1–10.
- Stockwell, D.R.B. & Peters, D.P. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science*, **13**, 143–158.
- Stockwell, D.R.B. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.
- Stoker, R.L., Ferris, D.K., Grant, W.E. & Folse, L.J. (1994) Simulating colonization by exotic species: a model of the red imported fire ant (*Solenopsis invicta*) in North America. *Ecological Modelling*, **73**, 281–292.
- Sutherst, R.W. & Maywald, G. (2005) A climate model of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae): implications of new regions, particularly Oceania. *Environmental Entomology*, **34**, 317–335.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgely, G.E., Miles, L., Ortega-Huerta,

- M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.
- Tucker, C.J. (1979) Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, **8**, 127–150.
- USGS (2001) *HYDRO1k elevation derivative database*. US Geological Survey, Washington, DC (<http://edcdaac.usgs.gov/gtopo30/hydro/>).

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