



SPECIAL
ISSUE

Model-based uncertainty in species range prediction

Richard G. Pearson^{1*}, Wilfried Thuiller², Miguel B. Araújo^{3,4,†}, Enrique Martinez-Meyer⁵, Lluís Brotons⁶, Colin McClean⁷, Lera Miles⁸, Pedro Segurado⁹, Terence P. Dawson¹⁰ and David C. Lees¹¹

¹Department of Herpetology and Center for Biodiversity and Conservation, American Museum of Natural History, New York, NY, USA, ²Laboratoire d'Ecologie Alpine UMR CNRS 5553 BP53, Grenoble Cedex 9, France, ³Biodiversity Research Group, Oxford University Centre for the Environment, Oxford, ⁴Biogeography and Conservation Laboratory, The Natural History Museum, London, UK, ⁵Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico City, Mexico, ⁶Centre Tecnològic Forestal de Catalunya, Pujada del Seminari s/n, Solsona, Catalunya, Spain, ⁷Environment Department, University of York, Heslington, York, ⁸UNEP World Conservation Monitoring Centre, Cambridge, UK, ⁹Unidade de Macroecologia e Conservação, Universidade de Évora, Estrada dos Leões, Évora, Portugal, ¹⁰Centre for the Study of Environmental Change and Sustainability, University of Edinburgh, Edinburgh, UK and ¹¹Entomology Department, The Natural History Museum, London, UK

*Correspondence: Richard G. Pearson, Department of Herpetology and Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA. E-mail: pearson@amnh.org

†Present address: Department of Biodiversity and Evolutionary Biology, National Museum of Natural Sciences, CSIC, C/José Gutiérrez Abascal, 2, 28006 Madrid, Spain.

ABSTRACT

Aim Many attempts to predict the potential range of species rely on environmental niche (or 'bioclimate envelope') modelling, yet the effects of using different niche-based methodologies require further investigation. Here we investigate the impact that the choice of model can have on predictions, identify key reasons why model output may differ and discuss the implications that model uncertainty has for policy-guiding applications.

Location The Western Cape of South Africa.

Methods We applied nine of the most widely used modelling techniques to model potential distributions under current and predicted future climate for four species (including two subspecies) of Proteaceae. Each model was built using an identical set of five input variables and distribution data for 3996 sampled sites. We compare model predictions by testing agreement between observed and simulated distributions for the present day (using the area under the receiver operating characteristic curve (AUC) and kappa statistics) and by assessing consistency in predictions of range size changes under future climate (using cluster analysis).

Results Our analyses show significant differences between predictions from different models, with predicted changes in range size by 2030 differing in both magnitude and direction (e.g. from 92% loss to 322% gain). We explain differences with reference to two characteristics of the modelling techniques: data input requirements (presence/absence vs. presence-only approaches) and assumptions made by each algorithm when extrapolating beyond the range of data used to build the model. The effects of these factors should be carefully considered when using this modelling approach to predict species ranges.

Main conclusions We highlight an important source of uncertainty in assessments of the impacts of climate change on biodiversity and emphasize that model predictions should be interpreted in policy-guiding applications along with a full appreciation of uncertainty.

Keywords

Bioclimate envelope modelling, biodiversity, Cape Flora, climate change, conservation biogeography, distribution modelling, environmental niche modelling, Proteaceae, South Africa, species biodiversity.

INTRODUCTION

Environmental niche models utilize associations between environmental variables and known species distributions to define abiotic conditions within which populations can be

maintained. Projection of modelled niches into new regions and under scenarios of future climate change enables the geographical distribution of suitable conditions to be predicted. This approach has been widely applied, including in studies investigating the potential impacts of climate change

on biodiversity (e.g. Peterson *et al.*, 2002; Midgley *et al.*, 2003; Thomas *et al.*, 2004; Hannah *et al.*, 2005; Thuiller *et al.*, 2005; Araújo *et al.*, 2006), conservation prioritization (e.g. Araújo & Williams, 2000; Ferrier *et al.*, 2002; Raxworthy *et al.*, 2003; Williams *et al.*, 2005), range filling (Svenning & Skov, 2004), niche evolution (Peterson *et al.*, 1999; Martínez-Meyer *et al.*, 2003; Graham *et al.*, 2004; Martínez-Meyer & Peterson, 2006), factors governing species distributions (Coudun & Gégout, 2006; Luoto *et al.*, 2006) and the geographical ecology of invasive species (Higgins *et al.*, 1999), agricultural pests (Baker *et al.*, 2000) and disease vectors (Costa *et al.*, 2002). However, whilst the modelling approach is generic, studies have employed a number of different techniques for defining potential ranges (e.g. Nix, 1986; Stockwell & Peters, 1999; Pearson *et al.*, 2002; Thuiller, 2003; Thuiller *et al.*, 2003; Miles *et al.*, 2004; Segurado & Araújo, 2004; McClean *et al.*, 2005; Maggini *et al.*, 2006) and the impact that the specific method has on model predictions is an important consideration in model applications (Thuiller *et al.*, 2004a).

Here we assess consistency in predictions from nine of the most widely applied environmental niche modelling approaches. Using identical input variables, each model was used to simulate current and potential future distributions for four species of Proteaceae that are endemic to South Africa's Cape Floristic Kingdom. We compare predictions by testing agreement between observed and simulated distributions, and by assessing consistency in predictions of changes in range size under future climates. Previous studies have demonstrated important differences between predictions arising from different data sample sizes (Stockwell & Peterson, 2002) and species range sizes (McPherson *et al.*, 2004; Segurado & Araújo, 2004). Our focus here is on differences between predictions from different modelling techniques (see also Loiselle *et al.*, 2003; Segurado & Araújo, 2004; Thuiller, 2004; Araújo *et al.*, 2005b). We highlight significant differences between models and demonstrate that the magnitude of variation between predictions can be very large. Further analysis of our results enables two key factors causing differences between model predictions to be identified: data input requirements and model extrapolation assumptions.

METHODS

The modelling approaches we tested were: artificial neural networks, with two alternative parameterizations, ANN1 (Pearson *et al.*, 2002) and ANN2 (Thuiller, 2003); the climate envelope range (CER) (Nix, 1986; similar to BIOCLIM); the constrained Gower metric (CGM) (Miles *et al.*, 2004; similar to DOMAIN); classification tree analysis (CTA) (Thuiller *et al.*, 2003); genetic algorithm (GA) (McClean *et al.*, 2005); the generalized additive model (GAM) (Segurado & Araújo, 2004); genetic algorithm for rule-set prediction (GARP) (Stockwell & Peters, 1999); and the generalized linear model (GLM) (Thuiller, 2003). Each modelling technique was implemented with close adherence to published studies (see Appendix S1 in Supplementary Material for details) and using the same five climatically derived input variables.

We studied a region of the Western Cape extending from 17°86'–20°79' E and 31°91'–34°83' S. Five model input variables considered to be critical to plant physiological function and survival were gridded for this region at a spatial resolution of 1' × 1' (Schulze, 1997; Midgley *et al.*, 2002). The variables used were mean minimum temperature of the coldest month, heat units calculated as the annual sum of daily temperatures (°C) exceeding 18 °C, annual potential evaporation (calculated as the sum of mean monthly A-pan equivalent potential evaporation figures derived using the Penman–Monteith method), winter soil moisture days and summer soil moisture days. Soil moisture days are calculated by a hydrological model and are defined as those days on which soil moisture is above a critical level for plant growth (Midgley *et al.*, 2002). Input variables under a climate warming scenario (IS92a) for 2030 were calculated using projections from the general circulation model HadCM2 interpolated to 1' × 1' resolution (as detailed in Schulze & Perks, 1999).

Two species and two subspecies whose distributions had contrasting spatial characteristics were selected so as to test model performance across a range of distribution types. Distributions were characterized by the number of occupied grid cells (occupancy) and the straight-line distance between the two most distant occupied grid cells (extent of occurrence) (Segurado & Araújo, 2004). The species studied were: *Diastella divaricata* subsp. *divaricata* (restricted area of occupancy and low extent of occurrence); *Leucospermum hypophyllocarpodendron* subsp. *hypophyllocarpodendron* (restricted area of occupancy and high extent of occurrence); *Leucospermum tomentosum* (large area of occupancy and low extent of occurrence); *Protea longifolia* (large area of occupancy and high extent of occurrence). The inclusion of two subspecies was considered appropriate since in each case the subspecies have distributional and functional characteristics that are strong enough to distinguish a taxonomic grouping that is driven by climate. *Leucospermum hypophyllocarpodendron* subsp. *hypophyllocarpodendron* is distinguished from its sister subspecies by the absence of leaf pubescence and differing leaf shape. These characteristics are associated with the less arid and cooler climate of the southern Cape lowlands, rather than the warmer western lowlands which are occupied by its sister. In the case of *D. divaricata* subsp. *divaricata*, this species is strongly distinguished from its sister by leaf size and shape, and is associated with the much warmer and drier conditions of the lowlands, rather than the cooler montane environment of its sister subspecies. In neither case are the subspecies sympatric with their sisters.

Species distributional data were available as presence and absence for 3996 sampled sites (Rebello, 1992). Each sampled site was located within a different 1' × 1' cell distributed across the gridded study region (total of 23,875 cells). Environmental niches were defined using each technique based on an identical randomly selected 70% of the sampled sites. The remaining 30% of the sampled data were used to test the agreement between modelled and observed distributions (Araújo *et al.*, 2005a). The 70:30 ratio of this random split approximately

follows the guidelines provided by Huberty (1994). We tested agreement between known presence/absence and simulated distribution by calculating the area under the receiver operating characteristic curve (AUC) and Cohen's kappa statistic of similarity (k) (Fielding & Bell, 1997; Pearce & Ferrier, 2000). We calculated the AUC using the method presented by Hanley & McNeil (1982) which is based on the derivation of the Wilcoxon statistic. This method of calculation is recommended for ecological applications because it is non-parametric (Pearce & Ferrier, 2000). Values of AUC range from 0.5 for models with no predictive ability to 1.0 for models giving perfect predictions. Kappa was calculated following the formula presented in Fielding & Bell (1997) and yields values ranging from 0.0 (no predictive ability) to 1.0 (perfect predictive ability).

The AUC and k have been widely applied to assess the predictive performance of species range models (e.g. Loiselle *et al.*, 2003; Thuiller, 2003; Brotons *et al.*, 2004; Huntley *et al.*, 2004; Parra *et al.*, 2004). The statistics may be interpreted according to subjective guidelines which suggest that AUC values above 0.9 (Swets, 1988) and k values above 0.7 (Monserud & Leemans, 1992) describe 'very good' discrimination ability. Unlike k , AUC is independent of species prevalence (the proportion of recorded presences relative to the number of sampled sites) and is thus the preferred statistic for comparing model performance across different species. AUC cannot, however, be calculated from the CER and GA output since these techniques predict presence/absence (the calculation of AUC requires model output to be a suitability, or probability, value scaled from 0 to 1). We thus use k to compare modelling techniques since this statistic can be calculated from either predicted presence/absence or from suitability values (by maximizing the statistic over a range of thresholds above which model outputs are considered to represent species presence). Despite being influenced by species prevalence, k is informative when comparing between techniques since the distributions on which each model was calibrated and tested were identical (i.e. prevalence was constant).

In order to predict potential ranges under current and future climate conditions we projected the niches defined by each technique onto the entire gridded study region. A decision threshold above which model outputs are considered to represent species presence was defined for those techniques that simulate a suitability value from 0 to 1 (all models except CER and GA). Thresholds were defined by maximizing agreement between observed and modelled distributions for the sampled dataset (3996 cells). Sensitivity (the proportion of true positive predictions vs. the number of actual positive sites) and specificity (the proportion of true negative predictions vs. the number of actual negative sites) were calculated at thresholds increasing in increments of 0.01 from 0 to 1, and the threshold at which these two values were closest was adopted. This approach balances the cost arising from an incorrect prediction against the benefit gained from a correct prediction (Manel *et al.*, 2001).

Having defined species ranges for the study region, we assessed the similarity between model predictions of change in

range size under future climates. For each technique, we calculated the percentage gain or loss of suitable climate-space from current to future modelled climate envelopes under two assumptions of species dispersal ability (Peterson *et al.*, 2002; Thomas *et al.*, 2004): firstly, we assumed unlimited dispersal, such that the future distribution is the entire area projected by the climate envelope model; secondly, we assumed no dispersal, whereby the future distribution is the overlap between current and future envelopes.

Finally, in order to test for similarity between predictions from different techniques, we used cluster analysis to group predicted ranges from different models under current and future climate conditions. Methods were grouped using average clustering based on Bray–Curtis dissimilarities (Clarke & Gorley, 2001) of model predictions combined for all four species. The significance of groupings was assessed with analysis of similarity (ANOSIM) (Clarke & Green, 1988) which tests the degree to which differences between groups are greater than differences within groups. Cluster analysis was carried out using PRIMER 5 software (<http://www.primer-e.com>).

RESULTS

Assessing consistency in model predictions

We first assessed consistency in model predictions by measuring agreement between modelled present-day distributions and known presence and absence of species (Table 1). Our results overall showed good ability to predict observed distributions, with AUC values ranging from 0.850 to 0.997. These statistics can be interpreted as indicating good predictive performance according to the guidelines of Swets (1988). However, variability in predictive performance between modelling techniques was high, with mean k varying by up to 0.259 between models. Results for estimates of change in range size under future climates also demonstrate that the modelling technique used to define climate envelopes can have a very large impact on predictions (Fig. 1). Predictions for three of the four species varied in both the direction (gain or loss) and magnitude of change. For example, for *L. hypophyllocarpodendron* subsp. *hypophyllocarpodendron* (Fig. 1b) under the assumption of unlimited dispersal, five models predicted an increase in range size and four models predicted a decrease, whilst with no dispersal (in which case suitable climate space cannot be gained) predicted losses ranged from 1–100%. Only for *P. longifolia* (Fig. 1d) did the models all predict the same direction of change, yet losses still ranged from 58–94% with unlimited dispersal, and 68–98% with no dispersal.

Grouping the techniques using cluster analysis identified a first group consisting of three methods (CTA, GAM and GLM), second and third groups comprising two methods each (ANN1 and ANN2; CER and GARP) and two methods with distinct predictions (CGM and GA). These clusters were consistent across current (ANOSIM global $R = 0.819$, significance = 0.2%) and future (ANOSIM global $R = 1.0$, significance = 0.1%) predictions. The identification of five distinct

Table 1 Assessment of agreement between modelled and observed distributions. Statistics given are area under the receiver operating characteristic curve (AUC) and Cohen's kappa (*k*)

Modelling technique	<i>D. divaricata</i> subsp. <i>divaricata</i>		<i>L. hypophyllo.</i> subsp. <i>hypophyllo.</i>		<i>L. tomentosum</i>		<i>P. longifolia</i>		Mean <i>k</i>
	AUC	<i>k</i>	AUC	<i>k</i>	AUC	<i>k</i>	AUC	<i>k</i>	
ANN1	0.995	0.780	0.888	0.350	0.996	0.853	0.918	0.515	0.625
ANN2	0.993	0.796	0.930	0.417	0.990	0.799	0.908	0.487	0.625
CER*	–	0.387	–	0.095	–	0.689	–	0.294	0.366
CGM*	0.988	0.748	0.941	0.353	0.993	0.754	0.890	0.398	0.563
CTA	0.950	0.628	0.857	0.350	0.920	0.736	0.879	0.456	0.543
GA*	–	0.480	–	0.210	–	0.567	–	0.409	0.417
GAM	0.995	0.745	0.931	0.366	0.997	0.842	0.920	0.498	0.613
GARP*	0.931	0.347	0.850	0.127	0.937	0.692	0.868	0.406	0.393
GLM	0.994	0.748	0.927	0.382	0.997	0.800	0.918	0.493	0.606
Mean AUC	0.969		0.896		0.976		0.890		

Values were calculated from model predictions made using a randomly selected 30% of the sampled data that were not used for defining environmental niches. Empty cells (–) are those for which AUC cannot be calculated (see Methods). An asterisk (*) identifies those models that use only observed species presence data, whilst those species without an asterisk use both observed presence and absence data.

patterns of range prediction from nine models highlights the differences between modelling approaches, whilst providing a foundation for further investigation as to which technique, or group of techniques, may be most appropriate for predicting future ranges.

Accounting for differences between model predictions

Variation between the identified groups of models may be understood, at least in part, with reference to two characteristics of the modelling techniques. Firstly, the five techniques of groups one and two used data about both the observed presence and absence of species, whilst the remaining four approaches used only observed presence records (which are the only data available in many applications). Although both approaches model the 'realized' niche of species in environmental space (since observed distribution data are used), presence/absence techniques project the niche model onto a geographical space whereby information regarding unsuitable conditions resulting from both biotic and abiotic limiting factors (Pearson & Dawson, 2003) is inherent within the absence data. In contrast, presence-only approaches project the realized niche into a geographical space without giving weight to observed absence information (Peterson *et al.*, 1999; Raxworthy *et al.*, 2003), resulting in a poorer fit to the current observed distribution (mean *k* for presence-only approaches = 0.435; mean *k* for presence/absence approaches = 0.602; see Table 1). Differences in predictions of changes in range size between presence/absence and presence-only techniques were statistically significant (Mann–Whitney U-test $P < 0.001$ for both unlimited dispersal and no dispersal), with a general tendency for presence-only techniques to predict greater losses. Thus, across all four species under the assumption of unlimited dispersal, presence/absence techniques predicted 13 range gains and 7 losses

(mean = 62% gain; range = 409%), compared with 1 gain and 15 losses (mean = 67% loss; range = 109%) for presence-only techniques. Similarly, with no dispersal, losses ranged from 0–93% with presence/absence models, and from 78–100% with presence-only models.

Secondly, differences between simulations from alternative models will be caused by the various assumptions made by each algorithm when extrapolating environmental variables beyond the range of the data used to define the modelled niche. Isolating instances of extrapolation in our study (19% of cells under the current climate and 56% of cells under future climate have at least one variable falling outside the range for which the environmental niche was modelled), we find that: GLM predicted 11% of these cases as 'presences'; GAM, CTA, ANN1 and ANN2 predicted 7%, 6%, 5% and 3%, respectively, as presences; GARP predicted < 0.2% as presences; CER, CGM and GA predicted no presences. The problem of extrapolation into 'unknown' niche space is rarely considered in model applications (Pearson & Dawson, 2003; Thuiller *et al.*, 2004b) yet we demonstrate the uncertainty that can arise if models are naively applied without consideration of the effect that extrapolation will have on model predictions.

DISCUSSION

Previous critiques have questioned the usefulness of the environmental niche modelling approach (Woodward & Beerling, 1997; Davis *et al.*, 1998; Lawton, 2000; Pearson & Dawson, 2003), citing a number of potential sources of predictive error that may be categorized as either 'algorithmic' or 'biotic' (Fielding & Bell, 1997). Algorithmic errors are caused by limitations of the modelling techniques and include the model-based uncertainty that we have identified and quantified here. Further algorithmic uncertainty is caused by the use of alternative methods for identifying decision thresholds (Pearson *et al.*, 2004; Liu *et al.*, 2005). Biotic errors

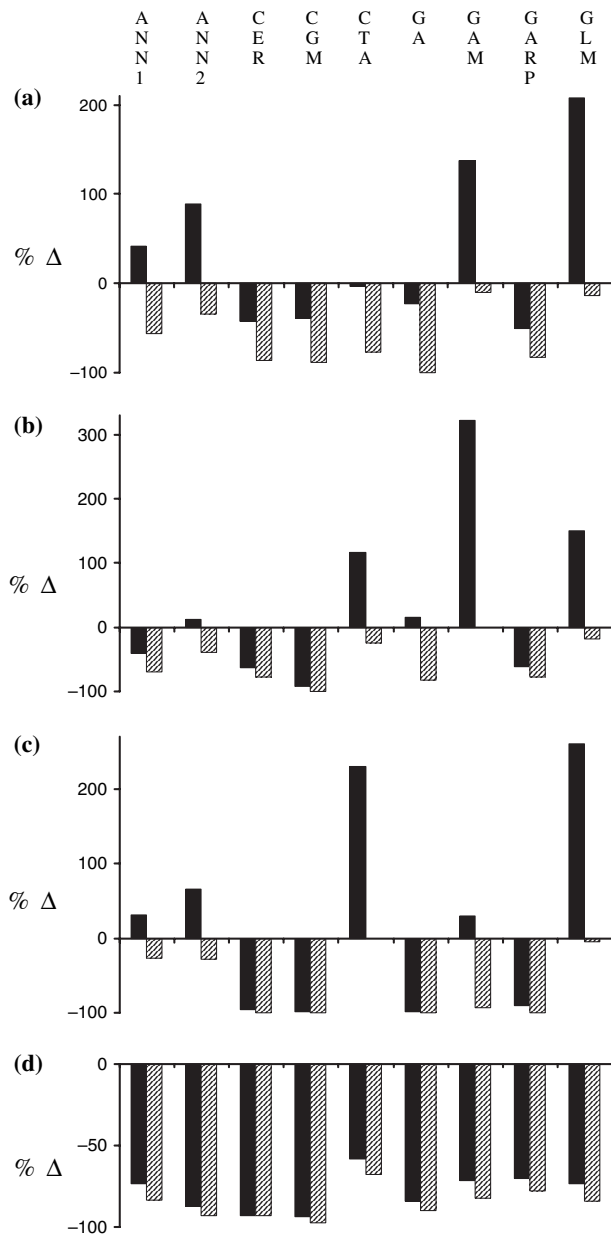


Figure 1 Comparison of predicted percentage gain/loss (%Δ) of suitable climate space by 2030 for four Proteaceae in the Cape using nine ecological niche modelling techniques (see Methods for explanation of model acronyms). Solid bars present results under the assumption of unlimited dispersal, and cross-hatched bars those with no dispersal: (a) *Diastella divaricata* subsp. *divaricata*; (b) *Leucospermum hypophyllocarpodendron* subsp. *hypophyllocarpodendron*; (c) *Leucospermum tomentosum*; (d) *Protea longifolia*.

are caused by ecological factors that are not captured within the niche-based modelling framework, which may cause species distributions to depart from assumptions of equilibrium that are inherent to niche-based models (Araújo & Pearson, 2005). Biotic uncertainty thus results from our limited understanding of factors including species dispersal ability (Pearson & Dawson, 2005), biotic interactions (Davis *et al.*, 1998), rapid *in situ* adaptation (Thomas *et al.*, 2001),

existing adaptation of populations to local conditions across the range (Hampe, 2004; Harte *et al.*, 2004) and the direct impacts of increased concentrations of atmospheric CO₂ on species physiology (e.g. Catovsky & Bazzaz, 1999). Further uncertainties result from potential inaccuracies in the available species distribution data sets (Griffiths *et al.*, 1999; Soberón & Peterson, 2004) and, perhaps most fundamentally in the case of climate change applications, uncertainties are inherent in predicted scenarios of future climate (Allen *et al.*, 2000). Despite these difficulties, it has been argued that environmental niche models provide the best available tool for rapid species-specific assessments of potential ranges (Baker *et al.*, 2000; Hannah *et al.*, 2002; Pearson & Dawson, 2003, 2004; Huntley *et al.*, 2004). Our results highlight the need for much further research to test and improve the approach so as to increase confidence in model predictions. By demonstrating large differences between predictions from alternative modelling approaches, our study shows that selecting the most appropriate modelling technique to address a particular question is a very important part of the modelling process.

Whilst we have demonstrated a great deal of variability in predictions from alternative models, it has not been possible to single out a 'best' technique for predicting potential species ranges. Comparing each model's ability to simulate observed presences and absences is an informative step, yet good model fits with observed distributions do not guarantee that a species' potential range has been accurately captured (Pearson & Dawson, 2003; Hampe, 2004; Araújo *et al.*, 2005a; Randin *et al.*, 2006). It may, in fact, be argued that the best techniques are those that make the fewest false-negative predictions (Anderson *et al.*, 2003). This is because predictions of unsuitability at sites where a species' presence has been observed are clear errors, whilst predictions of suitability at sites where no presence has been observed can be attributed to non-climatic factors that limit the actual distribution (i.e. biotic error) or to insufficient sampling (Anderson, 2003). Further research to test the various modelling approaches, including analysis of variability using alternative decision thresholds that minimize false-negative predictions (Pearson *et al.*, 2004), assessment of the ability to predict past distribution changes (Martinez-Meyer *et al.*, 2004; Martínez-Meyer & Peterson, 2006) and near future (Araújo *et al.*, 2005b) distribution changes, and comparison against predictions from mechanistic models (Cramer *et al.*, 2001), will be required to decipher which technique, or group of techniques, is most appropriate for range prediction in different applications.

Our study has highlighted two key factors that should be carefully considered in applications of environmental niche models, namely data input requirements (presence/absence vs. presence-only data) and model extrapolation assumptions. The impacts that such factors have on model results must be investigated and taken into account when drawing conclusions from niche-based models across different applications (Loiselle *et al.*, 2003). We recommend that methodologies to avoid model extrapolation are adopted (Pearson *et al.*, 2002) and that future studies investigate predictions obtained from a

range of modelling techniques so as to reduce and quantify predictive uncertainty (Araújo *et al.*, 2005b, 2006; Thuiller *et al.*, 2005). However, that is not to say that application of a single technique cannot provide informative biogeographical data, so long as model behaviour is well understood and can be justified for the application at hand (e.g. Raxworthy *et al.*, 2003). Perhaps most importantly, it is vital that environmental niche models are interpreted as tools for sharpening our understanding of species range constraints, and that they are only applied in a predictive capacity along with full appreciation of the inherent uncertainty.

ACKNOWLEDGEMENTS

We thank G.F. Midgley for data provision and advice regarding species characteristics, and L. Hannah for logistical support and collaboration. We are grateful to A.T. Peterson and P.M. Berry for commenting on the manuscript, and to anonymous referees for their suggestions. The workshop that initiated this study in 2002 was partially funded by the Center for Applied Biodiversity Science of Conservation International, and was hosted by Centre d'Ecologie Fonctionnelle et Evolutive (CEFE)-CNRS UMR 5175, Montpellier, France. Research by R.G.P. was supported by the Environmental Change Institute, University of Oxford. Research by R.G.P., W.T. and M.B.A. was supported by EC FP6 ALARM project (GOCE-CT-2003-506675).

REFERENCES

- Allen, M.R., Stott, P.A., Mitchell, J.F.B., Schnur, R. & Delwort, D.L. (2000) Quantifying the uncertainty in forecasts of anthropogenic climate change. *Nature*, **407**, 617–620.
- Anderson, R.P. (2003) Real vs. artefactual absences in species distributions: tests for *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. *Journal of Biogeography*, **30**, 591–605.
- 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.
- Araújo, M.B. & Pearson, R.G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693–695.
- Araújo, M.B. & Williams, P.H. (2000) Selecting areas for species persistence using occurrence data. *Biological Conservation*, **96**, 331–345.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005a) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo, M.B., Whittaker, R.J., Ladle, R.J. & Erhard, M. (2005b) Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, **14**, 529–538.
- Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2006.01482.x.
- Baker, R.H.A., Sansford, C.E., Jarvis, C.H., Cannon, R.J.C., Macleod, A. & Walters, K.F.A. (2000) The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agriculture, Ecosystems and Environment*, **82**, 51–71.
- Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, **27**, 437–448.
- Catovsky, S. & Bazzaz, F.A. (1999) Elevated CO₂ influences the response of two birch species to soil moisture: implications for forest community structure. *Global Change Biology*, **5**, 507–518.
- Clarke, K.R. & Gorley, R.N. (2001) *Primer v5: user manual/tutorial*. PRIMER-E, Plymouth.
- Clarke, K.R. & Green, R.H. (1988) Statistical design analysis for a 'biological effects' study. *Marine Ecology Progress Series*, **46**, 213–226.
- Costa, J., Peterson, A.T. & Beard, C.B. (2002) Ecological niche modelling and differentiation of populations of *Triatoma brasiliensis* Neiva, 1911, the most important Chagas disease vector in northeastern Brazil (Hemiptera, Reduviidae, Triatominae). *American Journal of Tropical Medicine and Hygiene*, **67**, 516–520.
- Coudun, C. & Gégout, J.C. (2006) Soil nutritional factors improve plant species distribution models: an illustration with *Acer campestre* (L.) in France. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2005.01443.x.
- Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A. & Young-Molling, C. (2001) Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Ferrier, S., Watson, G., Pearce, J. & Drielsma, M. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. *Biodiversity and Conservation*, **11**, 2275–2307.
- 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.
- Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J. & Moritz, C. (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution*, **58**, 1781–1793.
- Griffiths, G.H., Eversham, B.C. & Roy, D.B. (1999) Integrating species and habitat data for nature conservation in Great Britain: data sources and methods. *Global Ecology and Biogeography*, **8**, 329–345.
- Hampe, A. (2004) Bioclimatic models: what they detect and what they hide. *Global Ecology and Biogeography*, **11**, 469–471.

- Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.
- Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, **11**, 485–495.
- Hannah, L., Midgley, G.F., Hughes, G. & Bomhard, B. (2005) The view from the Cape: extinction risk, protected areas, and climate change. *Bioscience*, **55**, 231–242.
- Harte, J., Ostling, A., Green, J.L. & Kinzig, A. (2004) Climate change and extinction risk. *Nature*, **430**, 33. doi:10.1038/nature02718.
- Higgins, S.L., Richardson, D.M., Cowling, R.M. & Trinder-Smith, T.H. (1999) Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology*, **13**, 303–313.
- Huberty, C.J. (1994) *Applied discriminant analysis*. Wiley Interscience, New York.
- Huntley, B., Green, R.E., Collingham, Y.C., Hill, J.K., Willis, S.G., Bartlein, P.J., Cramer, W., Hagermeijer, W.J.M. & Thomas, C.J. (2004) The performance of models relating species geographic distributions to climate is independent of trophic level. *Ecology Letters*, **7**, 417–426.
- Lawton, J.H. (2000) Concluding remarks: a review of some open questions. *Ecological consequences of heterogeneity* (ed. by M.J. Hutchings, E. John & A.J.A. Stewart), pp. 401–424. Cambridge University Press, Cambridge.
- Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.
- Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G. & Williams, P.H. (2003) Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology*, **17**, 1591–1600.
- Luoto, M., Heikkinen, R.K., Pöyry, J. & Saarinen, K. (2006) Determinants of biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2005.01395.x.
- Maggini, R., Lehmann, A., Zimmerman, N. & Guisan, A. (2006). Improving generalized regression analysis for spatial predictions of forest communities. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2006.01465.x.
- Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presences-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921–931.
- Martinez-Meyer, E. & Peterson, A.T. (2006) Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography*, in press.
- Martinez-Meyer, E., Peterson, A.T. & Navarro-Sigüenza, A.G. (2003) Evolution of seasonal ecological niches in the *Passerina* buntings (Aves: Cardinalidae). *Proceedings of the Royal Society of London Series B, Biological Sciences*, **271**, 1151–1157.
- Martinez-Meyer, E., Peterson, A.T. & Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, **13**, 305–314.
- McClellan, C., Lovett, J.C., Küper, W., Hannah, L., Sommer, J.H., Barthlott, W., Termansen, M., Smith, G.F., Tokumine, S. & Taplin, J.R.D. (2005) African plant diversity and climate change. *Annals of the Missouri Botanical Garden*, **92**, 139–152.
- McPherson, J.M., Jetz, W. & Rogers, D.J. (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology*, **41**, 811–823.
- Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C. & Powerie, L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, **11**, 445–451.
- Midgley, G.F., Hannah, L., Millar, D., Thuiller, W. & Booth, A. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation*, **112**, 87–97.
- Miles, L., Grainger, A. & Phillips, O. (2004) The impact of global climate change on tropical forest biodiversity in Amazonia. *Global Ecology and Biogeography*, **6**, 553–565.
- Monserud, R.A. & Leemans, R. (1992) Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling*, **62**, 275–293.
- Nix, H.A. (1986) A biogeographic analysis of Australian elapid snakes. *Atlas of elapid snakes* (ed. by R. Longmore), pp. 4–15. Australian Government Publishing Service, Canberra.
- Parra, J.L., Graham, C.C. & Freile, J.F. (2004) Evaluating alternative data sets for ecological niche models of birds in the Andes. *Ecography*, **27**, 350–360.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pearson, R.G. & Dawson, T.P. (2004) Bioclimate envelope models: what they detect and what they hide – response to Hampe (2004). *Global Ecology and Biogeography*, **13**, 471–473.
- Pearson, R.G. & Dawson, T.P. (2005) Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation*, **123**, 389–401.
- Pearson, R.G., Dawson, T.P., Berry, P.M. & Harrison, P.A. (2002) SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological Modelling*, **154**, 289–300.
- Pearson, R.G., Dawson, T.P. & Liu, C. (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography*, **27**, 285–298.
- Peterson, A.T., Soberon, J. & Sanchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265–1267.

- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R.W. & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2006.01466.x.
- Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. & Peterson, A.T. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, **426**, 837–841.
- Rebello, A.G. (1992) *Protea atlas manual: instruction booklet to the Protea Atlas Project*. National Botanical Institute, Claremont, South Africa.
- Schulze, R.E. (1997) *South African atlas of agrohydrology and climatology*. Report TT82/96, Water Research Commission, Pretoria.
- Schulze, R.E. & Perks, L.A. (1999) *Assessment of the impact of climate*. School of Bioresources Engineering and Environmental Hydrology, University of Natal, Pietermaritzburg.
- Segurado, P. & Araújo, M.B. (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography*, **31**, 1555–1568.
- Soberón, J. & Peterson, A.T. (2004) Biodiversity informatics: managing and applying primary biodiversity data. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **359**, 689–698.
- Stockwell, D.R.B. & Peters, D.P. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Systems*, **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.
- Svenning, J.-C. & Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters*, **7**, 565–573.
- Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285–1293.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt, L. (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siquira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., 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. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, **10**, 1–8.
- Thuiller, W., Vaydera, J., Pino, J., Sabate, S., Lavorel, S. & Garcia, C. (2003) Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). *Global Ecology and Biogeography*, **12**, 313–325.
- Thuiller, W., Araújo, M.B., Pearson, R.G., Whittaker, R.J., Brotons, L. & Lavorel, S. (2004a) Uncertainty in predictions of extinction risk. *Nature*, **430**, 33. doi: 10.1038/nature02716.
- Thuiller, W., Brotons, L., Araújo, M.B. & Lavorel, S. (2004b) Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, **31**, 165–172.
- 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 of the United States of America*, **102**, 8245–8250.
- Williams, P.H., Hannah, L., Andelman, S.J., Midgley, G.F., Araújo, M.B., Hughes, G., Manne, L.L., Martinez-Meyer, E. & Pearson, R.G. (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, **19**, 1063–1074.
- Woodward, F.I. & Beerling, D.J. (1997) The dynamics of vegetation change: health warnings for equilibrium 'dodo' models. *Global Ecology and Biogeography*, **6**, 413–418.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from <http://www.Blackwell-Synergy.com>.

Appendix S1 Implementation of the modelling techniques

BIOSKETCH

Richard Pearson is a post-doctoral fellow at the American Museum of Natural History where he is associated with both the Center for Biodiversity and Conservation and the Department of Herpetology. Richard's research falls principally within the fields of biogeography and spatial ecology, with a current focus being the development and application of species distribution (environmental niche) modelling approaches.

Editor: Mark Bush

This paper is part of the Special Issue on Species distribution modelling: methods, challenges and applications, which owes its origins to the workshop on Generalized Regression Analyses and Spatial Predictions: Grasping Ecological Patterns from Species to Landscape held at the Centre Pro Natura Aletsch in Riederalp, Switzerland, in August 2004.