



# Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition

E. Martínez-Meyer<sup>1\*</sup> and A. T. Peterson<sup>2</sup>

<sup>1</sup>Instituto de Biología, Universidad Nacional Autónoma de México, México, DF 04510, México and <sup>2</sup>Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, KS 66045, USA

## ABSTRACT

**Aim** To provide a test of the conservatism of a species' niche over the last 20,000 years by tracking the distribution of eight pollen taxa relative to climate type as they migrated across eastern North America following the Last Glacial Maximum (LGM).

**Location** North America.

**Methods** We drew taxon occurrence data from the North American pollen records in the Global Pollen Database, representing eight pollen types – all taxa for which  $\geq 5$  distinct geographic occurrences were available in both the present day and at the LGM (21,000 years ago  $\pm$  3000 years). These data were incorporated into ecological niche models based on present-day and LGM climatological summaries available from the Palaeoclimate Modelling Intercomparison Project to produce predicted potential geographic distributions for each species at present and at the LGM. The output for each time period was projected onto the 'other' time period, and tested using independent known occurrence information from that period.

**Results** The result of our analyses was that all species tested showed general conservatism in ecological characteristics over the climate changes associated with the Pleistocene-to-Recent transition.

**Main conclusions** This analysis constitutes a further demonstration of general and pervasive conservatism in ecological niche characteristics over moderate periods of time despite profound changes in climate and environmental conditions. As such, our results reinforce the application of ecological niche modelling techniques to the reconstruction of Pleistocene biodiversity distribution patterns, and to project the future potential distribution range of species in the face of global-scale climatic changes.

## Keywords

Climate change, North America, ecological niche modelling, evolutionary conservatism, plant migration, Pleistocene, pollen.

\*Correspondence: E. Martínez-Meyer, Instituto de Biología, Universidad Nacional Autónoma de México, México, DF 04510, México.  
E-mail: emm@ibiologia.unam.mx

## INTRODUCTION

Ongoing processes of climate change are affecting numerous aspects of the physical environment world-wide (Goudie, 2001; Bronstert, 2003; Diaz *et al.*, 2003a,b; Laternser & Schneebeli, 2003). Although general tendencies are towards warming by a few degrees, global climate change involves reorganization of many aspects of climate (Karl *et al.*, 1996; Houghton *et al.*,

2001), creating new contexts for biodiversity and natural systems. This complexity leads to uncertainty as to how Earth's ecosystems will evolve in human and natural dimensions over the coming decades.

Efforts to understand the implications of climate change for biodiversity have proceeded along two general lines. First, documentation of changes in geographic and ecological ranges (temporal and spatial) that have already begun and appear to

be increasingly pervasive (Parmesan, 1996; Brown *et al.*, 1997; Parmesan *et al.*, 1999; Walther *et al.*, 2002; Parmesan & Yohe, 2003). Second, use of climate projections (McFarlane *et al.*, 1992; Flato *et al.*, 1999; Pope *et al.*, 2002) as a basis for modelling effects on ecosystem processes (Rastetter, 1996; Cramer *et al.*, 2001; Melillo *et al.*, 2001; Karnosky, 2003) and the likely effects on individual species (Kadmon & Heller, 1998; Gottfried *et al.*, 1999; Bakkenes *et al.*, 2002; Erasmus *et al.*, 2002; Midgey *et al.*, 2002; Peterson *et al.*, 2002; Roura-Pascual *et al.*, 2005).

The species-specific models cited above focus on identifying associations between a species' known occurrences and the ecological (climatological) 'landscape', and then projecting those associations onto climatological data sets describing expected conditions at points in the future (e.g. for 2050). As such, the projections depend critically on the assumption that the occurrence–climate association (hereafter the ecological niche) does not change radically (Peterson *et al.*, 2005), which would remove any predictivity regarding the species' potential future distribution. This assumption has received some testing (Huntley *et al.*, 1989; Peterson *et al.*, 1999; Martínez-Meyer, 2002; Peterson, 2003; Martínez-Meyer *et al.*, 2004). If this assumption is not valid, the predictive power of models to project range changes would be undermined.

The present contribution represents a further test of the conservatism of ecological niche characteristics. Specifically, we use 'longitudinal' tests (i.e. tracking the same species through time), asking whether the modelled ecological niche of a species at one time is able to predict the known distribution of the species at another time, after a profound climate change event, and vice versa. This study represents one of few such studies of which we are aware (Hugall *et al.*, 2002; Hilbert *et al.*, 2004; Martínez-Meyer *et al.*, 2004), and focuses on North American plants (mostly trees), which in themselves have implications for the continent-wide dynamics of vegetation types.

## METHODS

Our analyses involved three steps: (1) modelling ecological niches for a single time period based on climatic parameters and known occurrences of the species; (2) projecting niche models onto modelled climates for a second time period; and (3) testing the ability of these models to predict known occurrences in the second time period. Tests were carried out both in geographic and ecological space, and (in the former) were repeated reversing predictor and predicted time periods.

### Input data

Ecological niches of plant species were modelled in eastern North America, with pollen records drawn from the Global Pollen Database (<http://www.ngdc.noaa.gov/paleo/gpd.html>) of the US National Geophysical Data Center. We analysed only those species for which  $\geq 5$  distinct geographic occurrences

(i.e. geographic coordinates differing by  $> 0.1^\circ$  of latitude or longitude) were available in both the present (as pollen records) and the Pleistocene [Last Glacial Maximum (LGM)  $\pm 3000$  years, 18,000–24,000 BP]. In all, only eight taxa fit the sample size criteria: *Acer rubrum*, *A. saccharum* type, *Alnus incana*, *A. viridis*, *Brasenia schreberi*, *Fraxinus nigra* type, *Juglans cinerea* and *Sarcobatus vermiculatus*; although some uncertainty exists in taxonomic identifications, we assume that the signal outweighs the noise, and that these errors do not detract from the utility of the data set. Sample sizes ranged from 5 to 7 points for LGM samples, and from 30 to 131 points for the present-day samples (Table 1).

Environmental variation in the present and the LGM was summarized in a series of GIS coverages ('layers') including aspects of climate and topography. The latter were derived from the USGS Hydro-1K data set (<http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html>), including slope, aspect and topographic index (elevation *per se* was excluded owing to the changing meaning of 'elevation' under different climates, although its derivatives listed above do not change in meaning). The former (climate data) were derived for present (1961–90) climates (New *et al.*, 1997) available from the Intergovernmental Panel on Climate Change (<http://www.ipcc.ch/>), and for LGM climates by the Palaeoclimate Modelling Intercomparison Project (<http://www-pcmdi.llnl.gov/pmip/>) (Hadley Climate Change Centre, HadCM2 scenario: cloud cover, annual mean temperature and annual mean precipitation). All geographic data sets were resampled to  $0.1^\circ$  resolution for analysis.

### Niche modelling

Niche models were developed using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell & Noble, 1992; Stockwell & Peters, 1999), specifically the DesktopGarp software package (<http://www.lifemapper.org/desktopgarp/>). GARP is designed to identify correlations between known species' occurrences and environmental parameters through an iterative process of rule selection, evaluation, testing, and incorporation or rejection. This process is achieved by a random 'evolutionary' process, in which solution space is explored via small mutations in rules delineating niche dimensions. Predictions were developed in a space defined only by climatic and topographic parameters; no spatial information was included in model development.

Within GARP, input occurrence data are divided into a series of subsets – when sample sizes permit (i.e. in models based on present-day pollen samples), a first 50% of occurrence points is set aside as extrinsic testing data (for evaluating the relative predictivity of the different models developed); the remainder of the points (or all of the points in the case of LGM occurrence data) is then divided into training data (for model development) and intrinsic testing data (for rule testing intrinsic to GARP processing). A method is chosen from a set of possibilities (logistic regression, BIOCLIM rules, etc.), applied to the data, and a rule developed (Stockwell & Peters,

**Table 1** Summary of reciprocal tests of predictivity of geographic distributions based on ecological niche characteristics for pollen records of eight plant species, predicting from Last Glacial Maximum ('Pleistocene') to present, and vice versa. Ten best-subsets models were developed for each reciprocal prediction for each species; 'all' refers to 10 of 10 models predicting presence, 'most' refers to >5 of 10 models predicting presence, and 'any' refers to at least 1 of 10 models predicting presence

Species	Proportional area predicted present			<i>n</i>	Number of test points successfully predicted			Binomial probability		
	All	Most	Any		All	Most	Any	All	Most	Any
Pleistocene predicts present										
<i>Acer rubrum</i>	0.178	0.272	0.438	103	58	75	88	$2.33 \times 10^{-15}$	0	$-8.4 \times 10^{-15}$
<i>Acer saccharum</i> type	0.170	0.394	0.772	131	82	116	130	$2.89 \times 10^{-15}$	0	$-2 \times 10^{-15}$
<i>Alnus incana</i>	0.247	0.457	0.720	101	49	63	92	$6.79 \times 10^{-8}$	0.000261	$5.28 \times 10^{-7}$
<i>Alnus viridis</i>	0.258	0.376	0.600	109	55	70	87	$1.04 \times 10^{-8}$	$5.11 \times 10^{-9}$	$3.06 \times 10^{-6}$
<i>Brasenia schreberi</i>	0.102	0.285	0.568	30	13	25	29	$3.88 \times 10^{-7}$	$5.09 \times 10^{-11}$	$4.27 \times 10^{-8}$
<i>Fraxinus nigra</i> type	0.391	0.629	0.886	112	80	104	111	$1.14 \times 10^{-12}$	$3.2 \times 10^{-14}$	$1.25 \times 10^{-6}$
<i>Juglans cinerea</i>	0.310	0.570	0.835	77	36	60	74	0.001284	$3.54 \times 10^{-5}$	0.000124
<i>Sarcobatus vermiculatus</i>	0.093	0.299	0.702	94	34	66	88	$2.19 \times 10^{-13}$	$2.78 \times 10^{-15}$	$3.01 \times 10^{-9}$
Present predicts Pleistocene										
<i>Acer rubrum</i>	0.115	0.163	0.236	6	5	5	5	$2.32 \times 10^{-6}$	$1.89 \times 10^{-5}$	0.000171
<i>Acer saccharum</i> type	0.079	0.142	0.235	6	2	4	4	0.008149	0.000305	0.00345
<i>Alnus incana</i>	0.029	0.149	0.277	7	0	2	5	0.184569	0.072542	0.002392
<i>Alnus viridis</i>	0.015	0.130	0.310	7	0	2	3	0.100394	0.050975	0.138968
<i>Brasenia schreberi</i>	0.070	0.140	0.230	6	2	4	6	0.005867	0.000289	$<10^{-10}$
<i>Fraxinus nigra</i> type	0.072	0.153	0.272	7	2	4	6	0.01038	0.001329	0.000109
<i>Juglans cinerea</i>	0.071	0.131	0.243	6	3	3	4	0.000337	0.003593	0.004081
<i>Sarcobatus vermiculatus</i>	0.145	0.219	0.282	5	3	4	4	0.001968	0.000501	0.001771

1999). Then, based on 1250 points resampled from the intrinsic testing data and 1250 points sampled randomly from areas across the study region at which the species is not known to occur, predictive accuracy is calculated as the sum of points actually present predicted as present and those actually absent predicted as absent, divided by the total number of points in the map. Once a rule set is generated, rules are 'evolved' and rules are evaluated again. Change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model. The algorithm runs either 1000 iterations or until addition of rules has no appreciable effect on the accuracy measure (convergence).

Geographic predictions can present two general types of error: omission (predicting areas of known presence as absent) and commission (predicting areas of absence as present). Because GARP generates distributional predictions based on a random-walk exploration of solution space, predictions vary somewhat from one run to the next, so we generated 100 models per species and filtered them based on error statistics to retain a 'best subset' (Anderson *et al.*, 2003). These models represent those from among the 100 models generated that present (1) minimum omission (the 20 models showing least omission based on overlay of the extrinsic testing data), and (2) intermediate estimates of area predicted present – because area predicted present can be taken as an index to commission error, we retained the 10 models showing least deviation from

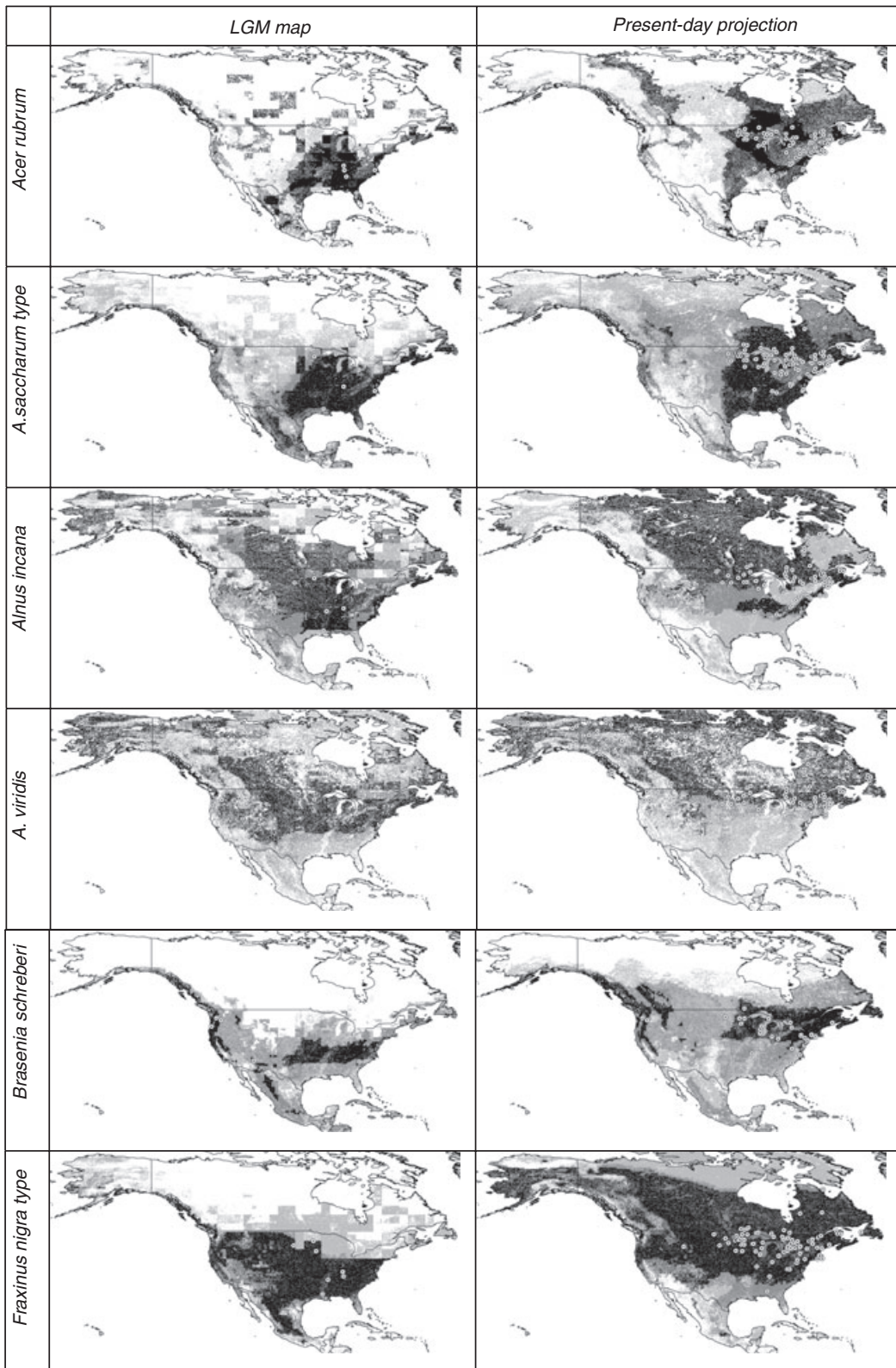
the median area among low-omission models (Anderson *et al.*, 2003). The sum of this 'best subset' of models was used as the single representative potential geographic prediction for the species.

### Testing model predictions

To test predictivity of species' ecology and distributions between time periods, we constructed niche models for each species for the present, and projected them on the Pleistocene climatic scenario. Pleistocene localities were then overlain onto the resulting projection, and statistical significance evaluated with a binomial test for each of three thresholds – 'any' model predicts ( $\geq 1$  of 10 models), 'most' models predict ( $> 5$  of 10 models), and 'all' models predict (10 of 10 models). The same process was followed to evaluate predictivity from Pleistocene to present: niche models were constructed for the Pleistocene and projected to the present-day climate conditions, present-day localities overlain, and statistical significance of this reciprocal prediction evaluated also with a binomial test, as follows:

$$P(r)_{\text{binomial}} = {}_n C_r p^r q^{n-r},$$

where  ${}_n C_r$  is the number of combinations of  $r$  successes out of  $n$  test occurrence points,  $r$  is the number of successful predictions in  $n$  test occurrence points, and  $p$  and  $q$  are the proportional areas predicted present and absent, respectively.



**Figure 1** Summary of model predictions based on Last Glacial Maximum (LGM) occurrence data and climate information, predicting present-day occurrences. White = predicted absent by all models, light grey = predicted present by any model, dark grey = predicted present by most models (6–10), and black = predicted present by all 10 models. Known occurrence points of pollen within each period (LGM and present) are overlain; note that the LGM points are those that were used to develop models, and the present points represent the independent testing data set.

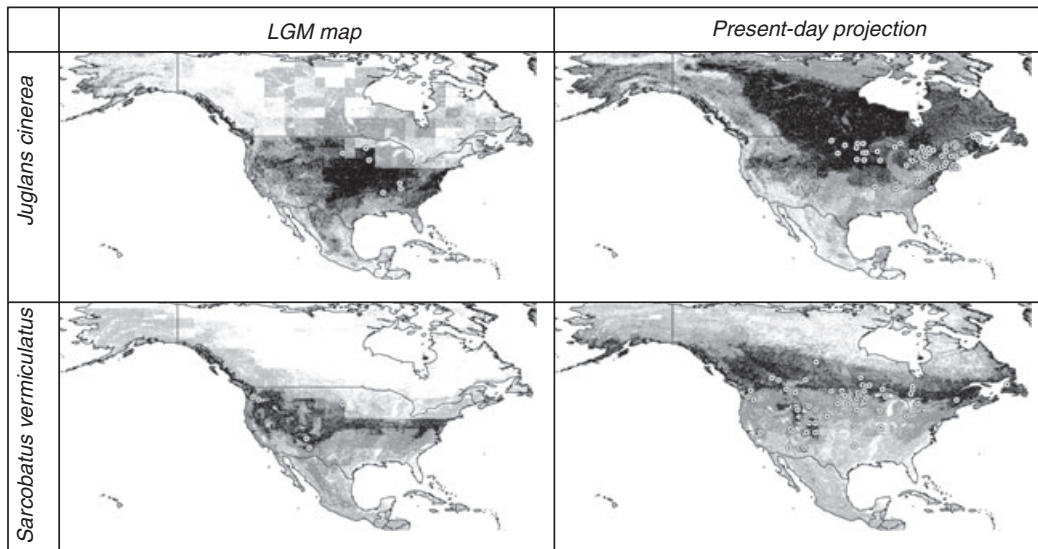


Figure 1 continued

Because the binomial test includes the proportional area predicted present as the ‘probability of success’, a cost of overprediction is incorporated, and the ‘easy’ solution of simply overpredicting massively to avoid omission error is thus removed. Because localities – particularly those from LGM – are well-separated spatially (all by >10 km), reductions in effective sample sizes owing to spatial autocorrelations are negligible. While these tests in geographic space are standard means of validating such model predictions (Fielding & Bell, 1997; Elith & Burgman, 2002; Scott *et al.*, 2002), ecological niche models should rightly be validated in ecological space to avoid pseudoreplication of test points (Soberón & Peterson, 2005). Although these validation methodologies are only now under development (A. T. Peterson and R. G. Pearson, unpublished data), we present a preliminary example here, based on the coincidence of test presence points *in ecological space* with portions of that space that are predicted present. Binomial tests were used to test whether this coincidence was better than that expected under a random model.

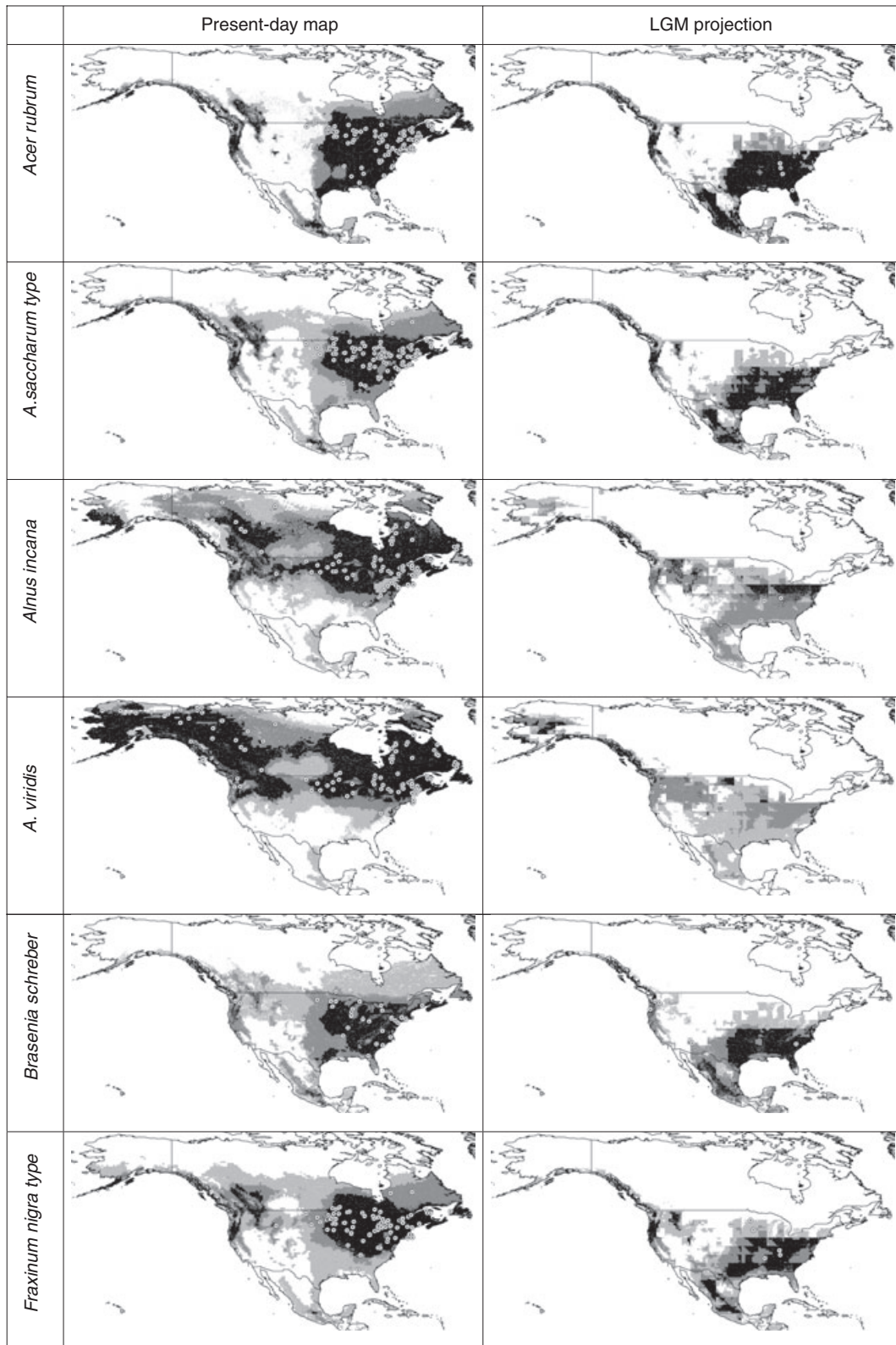
## RESULTS

Distributional patterns indicated by the ecological niche models developed in this study were highly predictive of actual patterns of occurrence (Figs 1 & 2). Although no direct test of model validity was developed *within* time periods, so as to conserve a maximum of point occurrences for developing and testing models, the distributions predicted nonetheless coincided well with known distributional patterns for each species and with the input data on which the models were based.

More importantly, however, all model predictions from one time period to the ‘other’ time period were highly statistically significant (Table 1), regardless of the threshold employed

(‘any’, ‘most’ or ‘all’). For example, for the Pleistocene LGM-based *Acer saccharum* type model at the ‘all’ models threshold, 82 of 131 points in the present were successfully predicted, although the model predicted only 17% of the area of study, yielding a binomial probability of  $2.89 \times 10^{-15}$ . Indeed, all of the LGM-predicts-present model projections were considerably more coincident with independent test points than would be expected at random (calculated similarly, all  $P < 0.002$ ; Table 1). For the converse (present-predicts-LGM models) testing model predictions was more difficult owing to small sample sizes, yet all predictions except *Alnus incana* at the ‘all’ and ‘most’ thresholds and *A. viridis* at all thresholds ( $P > 0.05$ ) were significantly more coincident with independent test points than random expectations ( $P < 0.05$ ). It should be noted that this test result indicates that the two niches were not statistically significantly different, but subtle differences may yet exist.

Looking at the example of *A. incana* predictions of present-day range projection based on a Pleistocene ecological niche model in ecological dimensions, a close coincidence exists between the test occurrence points and the portion of ecological space predicted present (Fig. 3). Of the total number of unique environmental combinations, 73.1% of them were predicted present by any of the best-subsets models, and 25.1% of them were predicted present by all 10 of the best-subsets models. Nonetheless, all seven of the independent test points fell within the area predicted by any of the best-subsets models, and four of seven of the independent test points fell within the area predicted by all best-subsets models, a level of coincidence that would be unexpected were the test points and prediction to be assorted at random with respect to one another (binomial test,  $P \ll 0.0001$  and  $P = 0.013$ , respectively). Although this test is preliminary in nature, it serves at least as an indication of a



**Figure 2** Summary of model predictions based on present-day occurrence data and climate information, predicting Last Glacial Maximum (LGM) occurrences. White = predicted absent by all models, light grey = predicted present by any model, dark grey = predicted present by most models (6–10), and black = predicted present by all 10 models. Known occurrence points of pollen within each period (LGM and present) are overlain; note that the present-day points are those that were used to develop models, and the LGM points represent the independent testing data set.

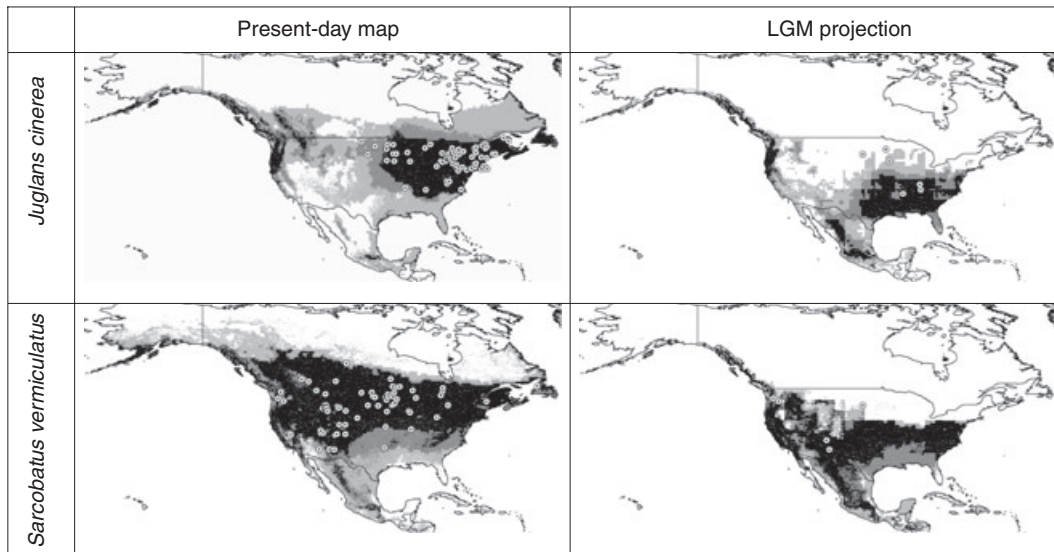
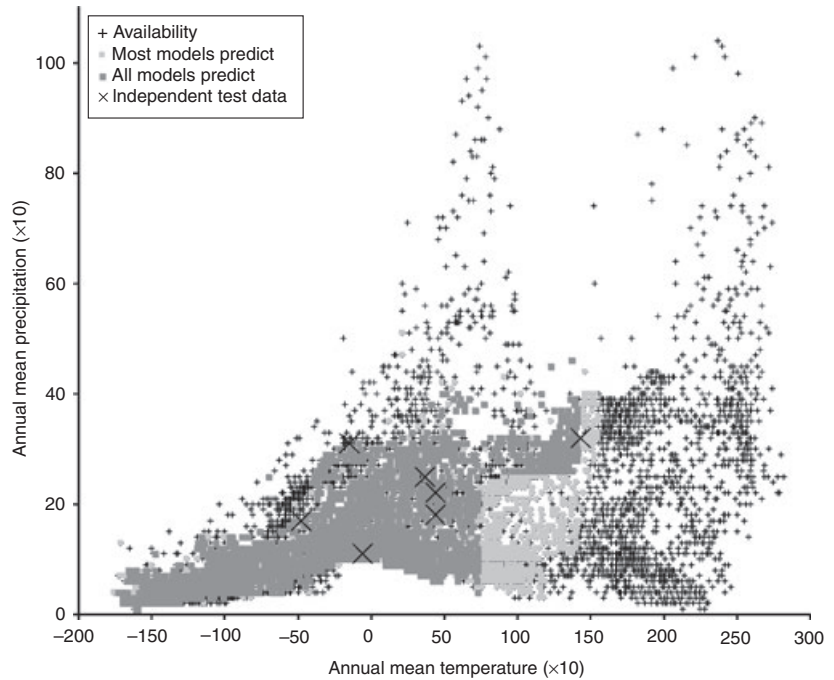


Figure 2 continued

**Figure 3** Exploratory test of the predicted and known distribution of *Alnus incana* in ecological space (annual mean precipitation in  $\text{cm} \times 10$  and annual mean temperature in  $^{\circ}\text{C} \times 10$ , shown for purposes of illustration). The ecological niche model was developed based on Last Glacial Maximum conditions and known occurrences. Black +s (in background) indicate the distribution of environmental combinations across North America. Areas of light and dark grey are areas predicted present by the ecological niche model for the species at low ( $\geq 5$  models predict) and high (all models predict), respectively. Black Xs indicate independent test presence points in present-day conditions.



non-random association between model predictions and independent test data in ecological space, as well as in geographic space.

## DISCUSSION

This study presents concrete indications that distributions of species are highly predictable, even before and after dramatic climate change events. We have demonstrated for eight plant species (all of those for which sample sizes were sufficient in the Global Pollen Database) that ecological characteristics of

LGM occurrences are highly successful in predicting the geographic distribution of the species 21,000 years later (present time), and vice versa. This result creates a picture of species following climate regimes faithfully as they migrate northward and southward during periods of changing climates.

This study is not the first to paint this picture. A previous study (Martínez-Meyer *et al.*, 2004) produced parallel results of excellent before-and-after predictivity for mammal species that survived the end of the Pleistocene. Several studies have now compared sister species pairs, and asked whether they can

predict one another's distributional patterns. Most of these studies (Huntley *et al.*, 1989; Peterson *et al.*, 1999; Martínez-Meyer, 2002) found that these species pairs are quite able to predict one another's distributions, suggesting niche conservatism over twice the time period since speciation, although a few (Martínez-Meyer, 2002; Rice *et al.*, 2003) seemed already to have differentiated ecologically between closely related species. Finally, the excellent predictivity of species' invasive distributions from their native-range ecological characteristics (Panetta & Dodd, 1987; Honig *et al.*, 1992; Higgins *et al.*, 1999; Sutherst *et al.*, 1999; Skov, 2000; Hoffmann, 2001; Peterson & Vieglais, 2001; Papes & Peterson, 2003; Peterson *et al.*, 2003a,b; Peterson & Robins, 2003; Iguchi *et al.*, 2004) suggests that the different community contexts in two distinct distributional areas do not affect species' distributions noticeably (Peterson, 2003).

This further testing of evolutionary conservatism of niche characteristics across dramatic climate change events opens the door to important applications of these techniques to pressing questions. For palaeoecology, these methods open the door to reconstruction of non-analogue past communities based on the autecological characteristics of each species individually. In the realm of historical biology, these results indicate that Pleistocene distributional areas of species will often be predictable based on present-day niche characteristics, offering very important tools for historical biogeography and for those attempting to understand speciation and patterns of differentiation across phylogeography (Rice *et al.*, 2003). In the conservation community, this further documentation of conservatism bolsters the case that projections of present-day niche models onto modelled future climate regimes offer useful information about species' potential geography after ongoing and future climate change processes take place.

The palaeoecological literature holds, of course, many examples of reconstruction of Pleistocene environments. Most commonly, samples of vegetative material or pollen are used to characterize biomes across broad regions (Wells, 1983; Jackson & Overpeck, 2000; Jackson *et al.*, 2000; Thompson & Anderson, 2000; Edwards *et al.*, 2003), which provides a broad brush-stroke picture of patterns of range shifts in changing climates. Some recent work has also focused on reconstructing more functional aspects of plant communities, such as percentage tree cover (Williams, 2002). The method presented here contrasts with previous efforts, in that individual species' ecological requirements and range shifts are modelled, rather than communities or functional types. This picture is probably best regarded as orthogonal to that produced by the other studies just cited: species apparently show quite individualistic behaviour under rapidly changing climates (Graham, 1975); these questions of ecological and geographic behaviour of species versus communities are an important priority for future analyses (Peterson *et al.*, 2005).

These analyses are intended as a first exploration of the ecological niches of species featured in the Global Pollen Database records, addressing the first-level question of whether predictivity exists among time periods longitudinally

within a fairly diverse suite of species. It should be noted that our models summarize *potential* distributional areas, and as such do not inform current debates regarding how quickly tree species were able to colonize distributional areas as they became suitable (McLachlan *et al.*, 2005). Clearly, it is important to broaden the coverage of palaeoclimatic models and scenarios used as the basis for past projections, given that different scenarios can paint quite different pictures of Pleistocene ecological landscapes.

Planned extensions of the analysis presented here involve application to understanding the historical biogeography of key tree species in forest communities, as well as to comparisons between models of global climate change effects on ecosystems and to species-based models of important plant species that make up key components of these same systems. These explorations suggest strongly that ecological niche modelling combined with modelled past-climate scenarios has much to offer to diverse aspects of organismal biology.

## ACKNOWLEDGEMENTS

This paper benefited greatly from discussions and interchange with Ricardo S. Pereira. Partial funding for this research was provided by the National Science Foundation.

## 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.
- Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemansand, R. & Latour, J.B. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390–407.
- Bronstert, A. (2003) Floods and climate change: interactions and impacts. *Risk Analysis* **23**, 545–557.
- Brown, J.H., Valone, T.J. & Curtin, C.G. (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 9729–9733.
- 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 CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.
- Diaz, H.F., Eischeid, J.K., Duncan, C. & Bradley, R.S. (2003a) Variability of freezing levels, melting season indicators, and snow cover for selected high-elevation and continental regions in the last 50 years. *Climatic Change*, **59**, 33–52.
- Diaz, H.F., Grosjean, M. & Graumlich, L. (2003b) Climate variability and change in high elevation regions: past, present and future. *Climatic Change* **59**, 1–4.

- Edwards, M.E., Hamilton, T.D., Elias, S.A., Bigelow, N.H. & Krumhardt, A.P. (2003) Interglacial extension of the boreal forest limit in the Noatak Valley, northwest Alaska: evidence from an exhumed river-cut bluff and debris apron. *Arctic, Antarctic, and Alpine Research*, **35**, 460–468.
- Elith, J. & Burgman, M. (2002) Predictions and their validation: rare plants in the Central Highlands, Victoria. *Predicting species occurrences: issues of scale and accuracy* (ed. by J.M. Scott, P.J. Heglund and M.L. Morrison), pp. 303–313. Island Press, Washington, DC.
- Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M. & Wessels, K.J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology*, **8**, 679–693.
- 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.
- Flato, G.M., Boer, G.J., Lee, W.G., McFarlane, N.A., Ramsden, D., Reader, M.C. & Weaver, A.J. (2000) The Canadian Center for Climate Modelling and Analysis Global Coupled Model and its climate. *Climate Dynamics*, **16**, 451–467.
- Gottfried, M., Pauli, H., Reiter, K. & Grabherr, G. (1999) A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity and Distributions*, **5**, 241–251.
- Goudie, A.S. (2001) The global distribution of dust storms: patterns and controls. *Annals of Arid Zone*, **40**, 303–315.
- Graham, A. (1975) Late Cenozoic evolution of tropical lowland vegetation in Veracruz, Mexico. *Evolution*, **29**, 723–735.
- Higgins, S.I., 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.
- Hilbert, D.W., Bradford, M., Parker, T. & Westcott, D.A. (2004) Golden bowerbird (*Prionodura newtonia*) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming. *Biological Conservation*, **116**, 367–377.
- Hoffmann, M.H. (2001) The distribution of *Senecio vulgaris*: capacity of climatic range models for predicting adventitious ranges. *Flora*, **196/5**, 395–403.
- Honig, M.A., Cowling, R.M. & Richardson, D.M. (1992) The invasive potential of Australian banksias in South-African fynbos – a comparison of the reproductive potential of *Banksia ericifolia* and *Leucadendron lauratum*. *Australian Journal of Ecology*, **17**, 305–314.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguera, M., der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (2001) *Climate Change 2001: the scientific basis*. Cambridge University Press, Cambridge.
- Hugall, A., Moritz, C., Moussalli, A. & Stanisci, J. (2002) Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosiphia bellendenkerensis* (Brazier 1875). *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 6112–6117.
- Huntley, B., Bartlein, P.J. & Prentice, I.C. (1989) Climatic control of the distribution and abundance of Beech (*Fagus* L.) in Europe and North America. *Journal of Biogeography*, **16**, 551–560.
- 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.
- Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the Late Quaternary. *Paleobiology*, **26**(Suppl.), 194–220.
- Jackson, S.T., Webb, R.S., Anderson, K.H., Overpeck, J.T., Webb III, T., Williams, J.W. & Hansen, B.C.S. (2000) Vegetation and environment in eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews*, **19**, 489–508.
- Kadmon, R. & Heller, J. (1998) Modelling faunal responses to climatic gradients with GIS: land snails as a case study. *Journal of Biogeography*, **25**, 527–539.
- Karl, T.R., Knight, R.W., Easterling, D.R. & Quayle, R.G. (1996) Indices of climate change for the United States. *Bulletin of the American Meteorological Society*, **77**, 279–292.
- Karnosky, D.F. (2003) Impacts of elevated atmospheric CO<sub>2</sub> on forest trees and forest ecosystems: knowledge gaps. *Environment International*, **29**, 161–169.
- Latenser, M. & Schneebeli, M. (2003) Long-term snow climate trends of the Swiss Alps (1931–99). *International Journal of Climatology*, **23**, 733–750.
- Martínez-Meyer, E. (2002) *Evolutionary trends in ecological niches of species*. PhD thesis. Department of Geography, University of Kansas, Lawrence, KS.
- Martínez-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.
- McFarlane, N.A., Boer, G.J., Blanchet, J.-P. & Lazare, M. (1992) The Canadian Climate Centre second-generation general circulation model and its equilibrium climate. *Journal of Climate*, **5**, 1013–1044.
- McLachlan, J.S., Clark, J.S. & Manos, P.S. (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, **86**, 2088–2098.
- Melillo, J.M., Janetos, A., Schimel, D. & Kittel, T. (2001) Vegetation and biogeochemical scenarios. *Climate change impacts on the United States: the potential consequences of climate variability and change* (ed. by J.M. Melillo, A.C. Janetos & T.R. Karl), pp. 73–91. Cambridge University Press, Cambridge.
- Midgely, G.E., Hannah, L., Millar, D., Rutherford, M.C. & Powrie, L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, **11**, 445–451.

- New, M., Hulme, M. & Jones, P. (1997) *A 1961–1990 mean monthly climatology of global land areas*. Climatic Research Unit, University of East Anglia, Norwich, UK.
- Panetta, F.D. & Dodd, J. (1987) Bioclimatic prediction of the potential distribution of skeleton weed *Chondrilla juncea* L. in Western Australia. *Journal of the Australian Institute of Agricultural Science*, **53**, 11–16.
- Papes, M. & Peterson, A.T. (2003) Predicting the potential invasive distribution for *Eupatorium adenophorum* Spreng. in China. *Journal of Wuhan Botanical Research*, **21**, 137–142.
- Parmesan, C. (1996) Climate and species' range. *Nature*, **382**, 765–766.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, J., Thomas, J.A. & Warren, M. (1999) Poleward shift of butterfly species' ranges associated with regional warming. *Nature*, **399**, 579–583.
- Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology*, **78**, 419–433.
- 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. & Vieglais, D.A. (2001) Predicting species invasions using ecological niche modeling. *BioScience*, **51**, 363–371.
- 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.H. & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.
- Peterson, A.T., Papes, M. & Kluza, D.A. (2003a) Predicting the potential invasive distributions of four alien plant species in North America. *Weed Science*, **51**, 863–868.
- Peterson, A.T., Scachetti-Pereira, R. & Kluza, D.A. (2003b) Assessment of invasive potential of *Homalodisca coagulata* in western North America and South America. *Biota Neotropica*, **3** (online journal), <http://www.biotaneotropica.org.br/v3n1/pt/abstract?article+BN00703012003>.
- Peterson, A.T., Tian, H., Martínez-Meyer, E., Soberon, J., Sánchez-Cordero, V. & Huntley, B. (2005) Modeling distributional shifts of individual species and biomes. *Climate change and biodiversity* (ed. by T.E. Lovejoy & L. Hannah), pp. 211–228. Yale University Press, New Haven, CT.
- Pope, V.D., Gallani, M.L., Rowntree, V.J. & Stratton, R.A. (2002) *The impact of new physical parametrizations in the Hadley Centre climate model – HadAM3*. Hadley Centre for Climate Prediction and Research, Bracknell, UK.
- Rastetter, E.B. (1996) Validating models of ecosystem response to global change. *BioScience*, **46**, 190–198.
- Rice, N.H., Martínez-Meyer, E. & Peterson, A.T. (2003) Ecological niche differentiation in the *Aphelocoma* jays: a phylogenetic perspective. *Biological Journal of the Linnean Society*, **80**, 369–383.
- Roura-Pascual, N., Suarez, A., Gómez, C., Pons, P., Touyama, Y., Wild, A.L. & Peterson, A.T. (2005) Geographic potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **271**, 2527–2535.
- Scott, J.M., Heglund, P.J. & Morrison, M.L. (2002) *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, DC.
- Skov, F. (2000) Potential plant distribution mapping based on climatic similarity. *Taxon*, **49**, 503–515.
- Soberon, 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. & Noble, I.R. (1992) Induction of sets of rules from animal distribution data: a robust and informative method of analysis. *Mathematics and Computers in Simulation*, **33**, 385–390.
- Stockwell, D.R.B. & Peters, D.P. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographic Information Systems*, **13**, 143–158.
- Sutherst, R.W., Maywald, G.F., Yonow, T. & Stevens, P.M. (1999) *CLIMEX user guide – Predicting the effects of climate on plants and animals*. CSIRO Publishing, Collingwood, Victoria, Australia.
- Thompson, R.S. & Anderson, K.H. (2000) Biomes of western North America at 18,000, 6000 and 0 <sup>14</sup>C yr BP reconstructed from pollen and packrat midden data. *Journal of Biogeography*, **27**, 555–584.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wells, P.V. (1983) Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. *Ecological Monographs*, **53**, 341–382.
- Williams, J.W. (2002) Variations in tree cover in North America since the Last Glacial Maximum. *Global and Planetary Change*, **35**, 1–23.

## BIOSKETCHES

**Enrique Martínez-Meyer** is a researcher at the Instituto de Biología, Universidad Nacional Autónoma de México. His research interests centre on the effects of environmental change on the distributions – ecological and geographic – of species.

**A. Townsend Peterson** is a Professor in the Department of Ecology and Evolutionary Biology, University of Kansas. His research interests revolve around distributions of species, in essence the question of why species are where they are and are not where they are not. For further information see <http://www.specifysoftware.org/Informatics/bios/biostownpeterson/>.

---

Editor: Mark B. Bush

This paper is part of the Special Issue, 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.