



The ice age ecologist: testing methods for reserve prioritization during the last global warming

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ABSTRACT

Aim We play the role of an ice age ecologist (IAE) charged with conserving biodiversity during the climate changes accompanying the last deglaciation. We develop reserve-selection strategies for the IAE and check them against rankings based on modern data.

Location Northern and eastern North America.

Methods Three reserve-selection strategies are developed. (1) Abiotic: the IAE uses no information about species–climate relationships, instead maximizing the climatic and geographic dispersion of reserves. (2) Species distribution models (SDMs): the IAE uses boosted-regression trees calibrated against pollen data and CCSM3 palaeoclimatic simulations from 21 to 15 ka BP to predict modern taxon distributions, then uses these as input to the ZONATION reserve-ranking program. (3) Rank-and-regress: regression models are used to identify climatic predictors of zonation rankings. All strategies are assessed against a ZONATION ranking based on modern pollen distributions. Analysis units are ecoregions and grid cells.

Results The abiotic strategy has a negative or no correlation between predicted and actual rankings. The SDM-based strategy fares better, with a significantly positive area-corrected correlation ($r = 0.474$, $P < 0.001$) between predicted and actual rankings. Predictive ability drops when grid cells are the analysis unit ($r = 0.217$, $P = 0.058$). Predictive ability for the rank-and-regress strategy is similar to the SDM results.

Main conclusions For the IAE, SDMs improve the predictive ability of reserve-selection strategies. However, predictive ability is limited overall, probably due to shifted realized niches during past no-analogue climates, new species interactions as species responded individually to climate change, and other environmental changes not included in the model. Twenty-first-century conservation planning also faces these challenges, and is further complicated by other anthropogenic impacts. The IAE's limited success does not preclude the use of climate scenarios and niche-based SDMs when developing adaptation strategies, but suggests that such tools offer at best only a rough guide to identifying possible areas of future conservation value.

Keywords

Climate change, niche models, no-analogue climates, palaeoecology, pollen, reserve selection, species distribution models, Zonation.

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INTRODUCTION

Imagine an ice age ecologist (IAE). She lives at the height of the last glacial period, 20,000 years ago, and is concerned about the threats to biodiversity posed by the coming deglaciation, global warming and other associated environmental changes. The IAE expects that species will shift distributions individually in response to climate change, and would like to establish a network of reserves designed to conserve 'future'¹ biodiversity. The goal of this reserve network is to give these species somewhere to go, i.e. to ensure that protected areas are set aside for habitat in the projected 'future' ranges of species. However, the IAE has limited resources, so she needs a strategy for prioritizing reserve selection.

The tools at the disposal of this hypothetical IAE are much like the ones we have today. She has data about the 'contemporary'¹ distributions of species and climates, earth system models that predict how the atmosphere, ocean and vegetation will respond to prescribed 'future' trajectories in various forcings to the earth system, niche-based species distribution models (SDMs) for predicting species distributions, and algorithms for ranking the conservation value of potential reserve locations.

Hundreds of papers have employed these combinations of data and models to predict species range shifts, patterns of biodiversity and extinction risk under 21st-century climate-change scenarios (e.g. reviews by Heikkinen *et al.*, 2006; Pereira *et al.*, 2010). However, the reliability of SDM-based predictions has been questioned (Botkin *et al.*, 2007; Dawson *et al.*, 2011), because of the non-trivial assumptions inherent to SDMs, e.g. that species distributions are in equilibrium with climate (Araújo & Pearson, 2005), that the chosen predictor variables are the key determinants of species distributions (Heikkinen *et al.*, 2006), that ecological niches are conserved (Peterson, 2011) and that spatial data can be used to predict temporal dynamics (Kharouba *et al.*, 2009). Nevertheless, SDMs are widely used to inform climate-adaptation strategies such as reserve selection and managed relocation (e.g. Hannah *et al.*, 2007; Hoegh-Guldberg *et al.*, 2008; Heller & Zavaleta, 2009).

The 21st-century predictions of SDMs can't be tested for decades. But the IAE's 'future' is our present, so we can use 20th-century observational data to evaluate the predictive ability of her reserve prioritization tools. The IAE analyses are designed to roughly parallel the kind of analyses that a modern conservation biologist might pursue, but because we are predicting from past to present, the IAE has several advantages and disadvantages relative to a modern ecologist (Table 1). The obvious disadvantage is that IAE's 'contemporary' occurrence datasets are based on fossil databases, which are usually sparser than modern occurrence datasets for a given species. Similarly,

¹In this paper, we use single quotes for 'contemporary' and 'future' when writing from the perspective of the IAE, for whom 'contemporary' is the last glacial period (21–15 ka BP) and 'future' is the 20th century (AD 1901–2000). No quotes means that we are following standard usage (i.e. from the perspective of a modern ecologist). Several words (particularly 'fossil' and 'modern') are strictly reserved for the modern ecologist's perspective.

the 'contemporary' climate datasets used by the IAE are palaeoclimatic simulations from general circulation models, which are less accurate and spatially coarser than the observed climate datasets available to modern ecologists. On the plus side, the IAE has a much more precise knowledge of the future than modern ecologists have. In particular, the IAE has an (ice) crystal ball that tells with high precision (e.g. for CO₂, ± 1 p.p.m. by volume, p.p.m.v.) the changes in greenhouse gas concentrations from the last glacial period to the present (e.g. Monnin *et al.*, 2001), while modern ecologists must rely on socioeconomic scenarios of greenhouse gas emissions (IPCC, 2007) that have a high uncertainty (e.g. for CO₂ by AD 2100, ± 200 p.p.m.v.). Other factors that confound niche-based models of 21st-century species range shifts (e.g. habitat conversion and fragmentation by humans, disequilibrium caused by slow rates of dispersal relative to rapid rates of climate change, etc.) tend to be less of an issue for the IAE (Table 1). These advantages and disadvantages should counterbalance to some degree, and so the IAE's reserve selection methods might be expected to be about as predictive as those by a modern ecologist for the 21st century, although the sources of uncertainty differ somewhat for the IAE and a modern ecologist.

There is a rich tradition of applying the long-term perspectives afforded by palaeodata to conservation biology and restoration ecology (e.g. Jackson & Hobbs, 2009; Willis *et al.*, 2010; Dawson *et al.*, 2011; Dietl & Flessa, 2011). Early versions of niche-based SDMs were applied to test the accuracy of climate model simulations and demonstrate that terrestrial species range shifts closely tracked historical climate change at time-scales ≥ 10³ years (Prentice *et al.*, 1991; Huntley *et al.*, 1993). Recently, there has been a rapid growth in 'hindcasting' simulations with SDMs (see review by Nogués-Bravo, 2009), designed to test biogeographic hypotheses about the temporal stability of species climatic niches (Martínez-Meyer & Peterson, 2006; Pearman *et al.*, 2008), the climatic predictors of extinction (Nogués-Bravo *et al.*, 2009), identify full-glacial refugia and post-glacial migration paths (Benito Garzón *et al.*, 2008; Waltari & Guralnick, 2009) and assess the effect of post-glacial dispersal limitations on species distributions and patterns of biodiversity (Svenning & Skov, 2007; Araújo *et al.*, 2008).

Here we go a step further, using the climate changes of the last glacial period as a way of testing the predictive ability of various reserve-selection strategies in the context of climate change and shifting distributions of plant taxa across North America. Three alternate reserve-ranking strategies are pursued (abiotic, SDM, and rank-and-regress) and then assessed by comparing the IAE's rankings of potential 'future' reserves with an independent set of reserve rankings that are based on actual data of late 20th-century taxon distributions.

DATA AND METHODS

Reserve-ranking strategies

In the abiotic strategy, the IAE uses none of her knowledge about 'contemporary' species distributions and species-climate

Table 1 Comparison of information available to the ice age ecologist (IAE) and modern ecologist (ME).

	Source of information		Advantage
	IAE	ME	
Input datasets			
'Contemporary' species occurrence data	Fossil occurrence data	Contemporary observational data	ME
'Contemporary' climates	Debiased and downscaled palaeoclimate simulations from global circulation models	Late 20th-century observed climates	ME
'Future' greenhouse gas trajectories	Ice core records	21st-century emission scenarios	IAE
'Future' insolation	Models of celestial mechanics	Models of celestial mechanics	Tie
'Future' ice extent, sea level rise, etc.	Geomorphological data	Modelled changes in sea level due to thermal expansion, glacier melt	Tie*
Validation datasets			
'Future' species occurrence data	Contemporary observational data	Unavailable	IAE
'Future' climates	Late 20th-century observed climates	Mid- to late 21st-century simulated climates	IAE
Factors confounding SDMs			
Natural and anthropogenic barriers to dispersal, habitat fragmentation, CO ₂ effects on plant physiology, evolutionary adaptation to climate change, etc.			Tie/IAE

*For the IAE, we can use data on actual past changes in sea level and ice extent, but the uncertainties in projected sea level rise and ice melt are not a major source of uncertainty in most distributional modelling of terrestrial species, except in coastal habitats.

relationships. Instead, she assumes that environmental diversity is a good proxy for biological diversity and so attempts to maximize the geographic and climatic dispersion of reserves. In this analysis, ecoregions are the basic unit of potential reserves. Two variants of the abiotic strategy were employed, one using predicted 'future' climates and the other using geographic variables. In the SDM strategy, the IAE uses her knowledge of 'contemporary' climates and species distributions to calibrate a boosted-regression-tree SDM (Elith *et al.*, 2008) and predict 'future' species distributions. The IAE then runs ZONATION (Moilanen *et al.*, 2005; Moilanen, 2007) to rank potential reserves based on the SDM predictions. One variant of the SDM analysis uses ecoregions as the unit of analysis, and the other uses grid cells of various resolutions. Lastly, in the rank-and-regress strategy, the IAE runs ZONATION for grid cells based on 'contemporary' species distributions and climates, then regresses these rankings against climate variables to identify predictors of high reserve rankings. She then uses this regression and her information about 'future' climates to rank potential 'future' reserves. The predictive abilities of the three strategies are assessed by comparing the IAE's 'future' reserve rankings with an independent set of ZONATION rankings based on actual taxon distributions at present. Appendix S1 in the Supporting Information gives further details about the implementation of these ranking strategies.

Data

'Contemporary' and 'future' climates

Information about the IAE's 'contemporary' climates (i.e. for 21–15 ka BP) was obtained from the SynTrace CCSM3

transient-climate simulations (Liu *et al.*, 2009). In these simulations, CCSM3 was run continuously from 22 ka BP to the 20th century, and the prescribed boundary conditions changed during the course of the model experiment. The prescribed changes were realistic, i.e. constrained by available information about actual trends in insolation, atmospheric greenhouse gas concentrations, sea level and coastline position, ice sheet extent and height and meltwater routing (Liu *et al.*, 2009). These simulations reproduce key climatic events during the last deglaciation (Liu *et al.*, 2009).

Seasonal temperatures and precipitation were extracted from the CCSM3 simulations for 22 time windows, spaced 1000 years (1 ka) apart: 21–20.9 ka BP, 20–19.9 ka BP, etc. The simulations for 21–14.9 ka BP serve as the 'contemporary' dataset for the IAE. CCSM3 data were available as decadal means of seasonal values of temperature and precipitation, for March, April and May (MAM), June, July and August (JJA), September, October and November (SON) and December, January and February (DJF). For each time window, 10 decadal means were averaged to provide a century-scale climatic mean. We debiased and downscaled the CCSM3 simulations from a native resolution of 3.75° × 3.75° to a 0.5° grid using a standard change-factor approach (Wilby *et al.*, 2004): palaeoclimatic simulations were differenced from the 0 ka BP simulation, then differences were bilinearly interpolated to the 0.5° grid and added to a baseline observational dataset for AD 1901–2000 from the University of East Anglia Climate Research Unit (CRU TS 3.0) (<http://badc.nerc.ac.uk>). For the CRU dataset, decadal means of seasonal temperature and precipitation values were created then averaged to create a mean for AD 1901–2000. This observational dataset also serves as the 'future' climate dataset for the IAE.

'Contemporary' and 'future' taxon distributions

The IAE's 'contemporary' and 'future' dataset of taxon occurrences for the late Pleistocene are based on gridded maps of pollen distributions for northern and eastern North America in which pollen abundances at individual records are temporally interpolated to intervals 1 ka apart then spatially interpolated to a 50-km grid (Williams *et al.*, 2004). This dataset has been used previously to generate biome maps and other palaeovegetation maps. Twenty-three pollen types were used: *Abies*, *Acer*, *Alnus*, *Ambrosia*, *Artemisia*, Asteraceae, *Betula*, *Carya*, Cupressaceae/Taxaceae, Cyperaceae, *Fagus*, *Fraxinus*, *Ostrya/Carpinus*, *Picea*, *Pinus strobus*, *Pinus* subg. *Pinus* (north-eastern US species), *Pinus* subg. *Pinus* (south-eastern US species), *Populus*, *Quercus*, Ranunculaceae, *Salix*, *Tsuga*, and *Ulmus*. Fossil pollen records for each 1-ka interval were matched to CCSM3 palaeoclimatic simulations for the same time interval, using the values from the 50-km pollen grid cell to the nearest 0.5° climate grid cell. Climate grid cells were not used to calibrate the boosted regression tree model if there were no pollen records present within that 0.5° cell for that time interval. The 'contemporary' calibration dataset used by the IAE's SDM and rank-and-regress strategies consists of the data for all 1-ka intervals from 21 to 15 ka BP. This 7000-year span stretches the IAE concept a bit, but has several advantages. Relatively few North American pollen records date to the Last Glacial Maximum (< 30 in this dataset), so adding more time windows provides a larger calibration dataset ($n = 289$). This time period was chosen to include a range of glacial climates from when Northern Hemisphere (NH) ice sheets were at their maximum extent (21–19 ka BP) to their initial melting as NH JJA insolation increased (19–15 ka BP), and the period ends before the abrupt NH warming and rapid ice ablation at 14.7 ka BP. This time period also includes no-analogue climates characterized by higher-than-present insolation and temperature seasonality (Williams & Jackson, 2007). Climate changes were relatively gradual prior to 15 ka, so the IAE can reasonably assume species distributions are roughly in equilibrium with climate. Pooling fossil data from multiple time windows also offers the chance to better encompass a species' fundamental niche (Nogués-Bravo, 2009; Nogués-Bravo *et al.*, 2009).

The 'future' dataset consists of the gridded pollen abundances for 0 ka BP (i.e. the late 20th century) from Williams *et al.* (2004) overlaid on the CRU observed-climate dataset. A species-occurrence dataset based on pollen abundances in recent sediments is preferable because the modern and fossil pollen data have been shaped by the same taphonomic processes of pollen transport, deposition and preservation. This 'future' dataset is reserved as a validation dataset for assessing the success of the reserve-selection strategies.

Tools*Species distribution models*

To predict species distributions as a function of climate, we used boosted regression trees (BRTs) (Elith *et al.*, 2008). BRTs are

based on decision-tree analysis, in which predictor variables are repeatedly partitioned into binary sets such that the within-set variance of the response variables is minimized. Decision trees are highly flexible with respect to data inputs, nonlinear relationships and interactions among variables, but can suffer from poor predictive ability. BRTs overcome this problem by linearly combining the predictions of many simple trees into a single predictive model (Elith *et al.*, 2008). BRTs have a high predictive ability relative to other SDMs (Elith *et al.*, 2006). The relative abundance of each taxon was used to calibrate the BRTs; models were fitted using a Poisson distribution. BRTs require prescribed parameters for tree complexity (the number of splits per tree) and learning rate (how quickly the model converges on a solution). Slow learning rates and high complexity tend to produce more complex models. Parameters were optimized by iteratively testing models with all combinations of tree complexities between one and five and learning rates using 0.01, 0.005 and 0.001. The parameters resulting in the lowest cross-validated deviance were chosen for predicting across time. For each taxon, the BRT predicts an estimated percent abundance per 0.5° grid cell. The predictive skill of BRTs was assessed using the cross-validated correlation between the 'contemporary' observed and predicted relative abundance of each taxon.

To assess which climate variables should be included in the BRTs, we began with 12 variables: mean temperature and precipitation for the four seasons and four bioclimatic variables – within-season diurnal temperature range (BIO2), temperature seasonality (standard deviation of mean temperature for the four seasons; BIO4), temperature annual range (maximum temperature of warmest season – minimum temperature of coldest season; BIO7), and precipitation seasonality (coefficient of variation across all four seasons; BIO15). Definitions of bioclimatic variables and codes follow the WorldClim dataset (<http://www.worldclim.org/>) but for seasonal data. We then narrowed the list of potential predictor variables by examining scatterplots of the relative abundance of a taxon and each climate variable, and retaining variables only if the scatter plots indicated that the variable seemed to constrain the taxon, e.g. the taxon only occurred in a subset of the available climate space. This pre-modelling variable selection was conducted separately for each taxon. Variable selection improved the predictive accuracy of the BRTs, based on experiments with the 0-ka data and BRTs using the full set of 12 variables versus those using the pre-selected list of variables. Although pre-modelling variable selection is an important component of the distributional modelling process, BRTs also internally incorporate variable selection because predictions are most heavily influenced by variables that explain the largest proportion of the variation in the data (Elith *et al.*, 2008).

ZONATION

ZONATION is a recently developed and popular algorithm for prioritizing sites for conservation (Moilanen *et al.*, 2005; Moilanen, 2007; Kremen *et al.*, 2008). ZONATION generates rankings by iteratively removing potential reserves based on their marginal value. For a given species j , the marginal value of reserve i ,

Q_{ij} is the proportion of the species' total abundance contained in reserve i . This calculation is done for all species in all potential reserves. We used the 'basic core-area' option in ZONATION, in which the overall marginal value of reserve i is calculated as the maximum across species, $\delta_i = \max(Q_{ij})$. In other words, a reserve's value is determined by the species for which the removal of the reserve has the greatest impact. The lowest ranking is assigned to the reserve with the smallest value of δ_i , and this reserve is then removed from consideration. This process is repeated until all reserves have been ranked from 1 to n , the total number of reserves. We did not place any additional constraints on the algorithm, such as differentially weighting species or spatial locations.

RESULTS

Predicted changes in climates and taxa distributions, 21 ka BP to the present

The magnitude of predicted climate changes between the last glacial period and the present, as simulated by CCSM3 (Fig. 1), are comparable to those projected for this century (IPCC, 2007). Across North America, JJA temperatures increased on average by 6.6 °C between 17 and 0 ka BP and DJF temperatures increased by 13.6 °C. Precipitation increased as well, by 8.0 mm in JJA and an 8.3 mm gain in DJF (Fig. 1).

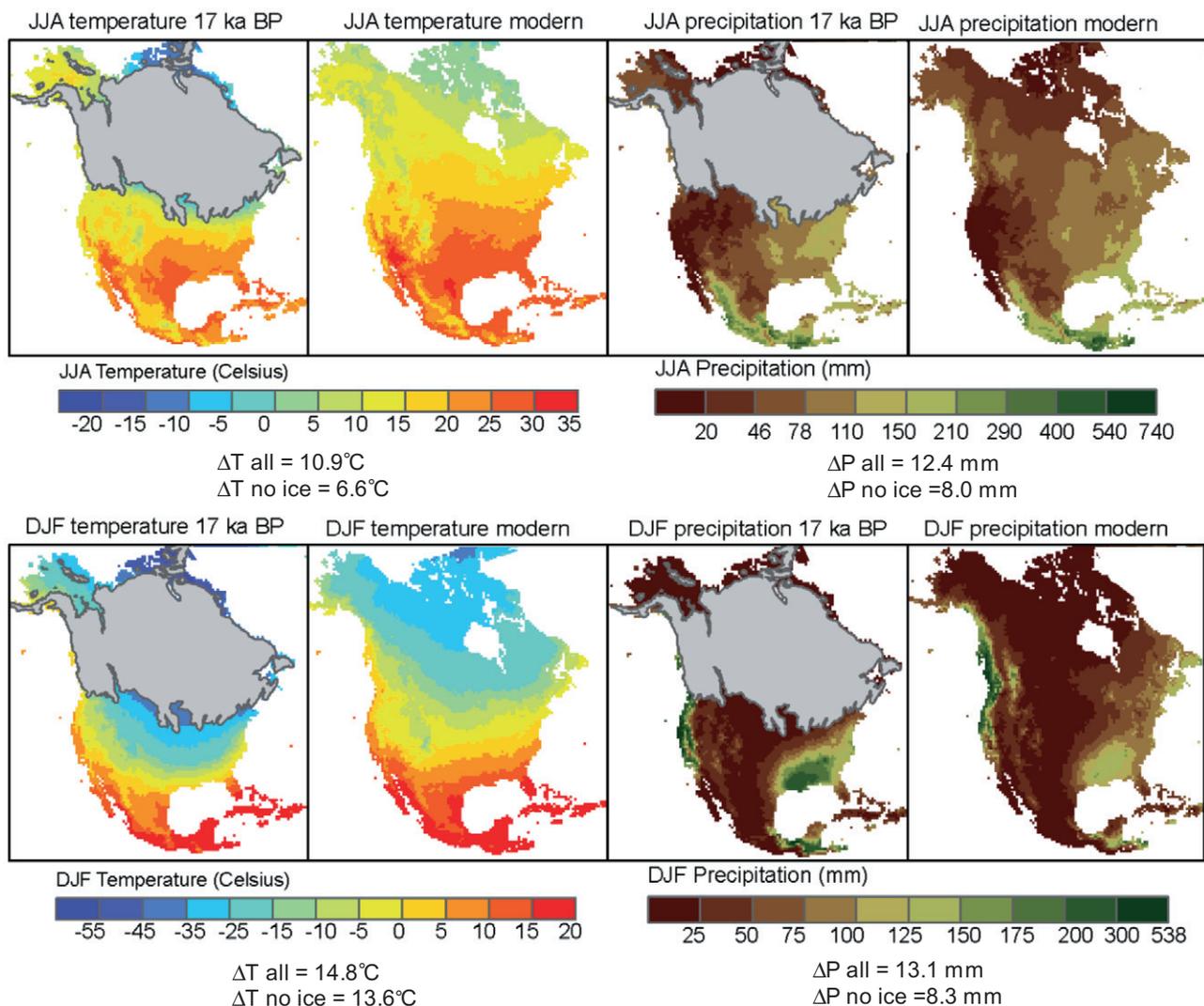


Figure 1 North American climates for 17 and 0 ka BP (17 ka BP was chosen as a representative time period between the 21–15 ka BP time window used for model calibration). Four variables are shown: mean temperatures for June, July and August (JJA), mean temperatures for December, January and February (DJF), mean JJA precipitation and mean DJF precipitation. Climate simulations for 17 ka BP are from the CCSM3 3.0 transient climate simulations performed by the SynTrace research consortium (Liu *et al.*, 2009). ' ΔT all' and ' ΔP all' refer to the average difference (17 ka BP – 0 ka BP) for all grid cells while ' ΔT no ice' and ' ΔP no ice' refers to the average difference across all grid cells not covered by ice at 17 ka BP.

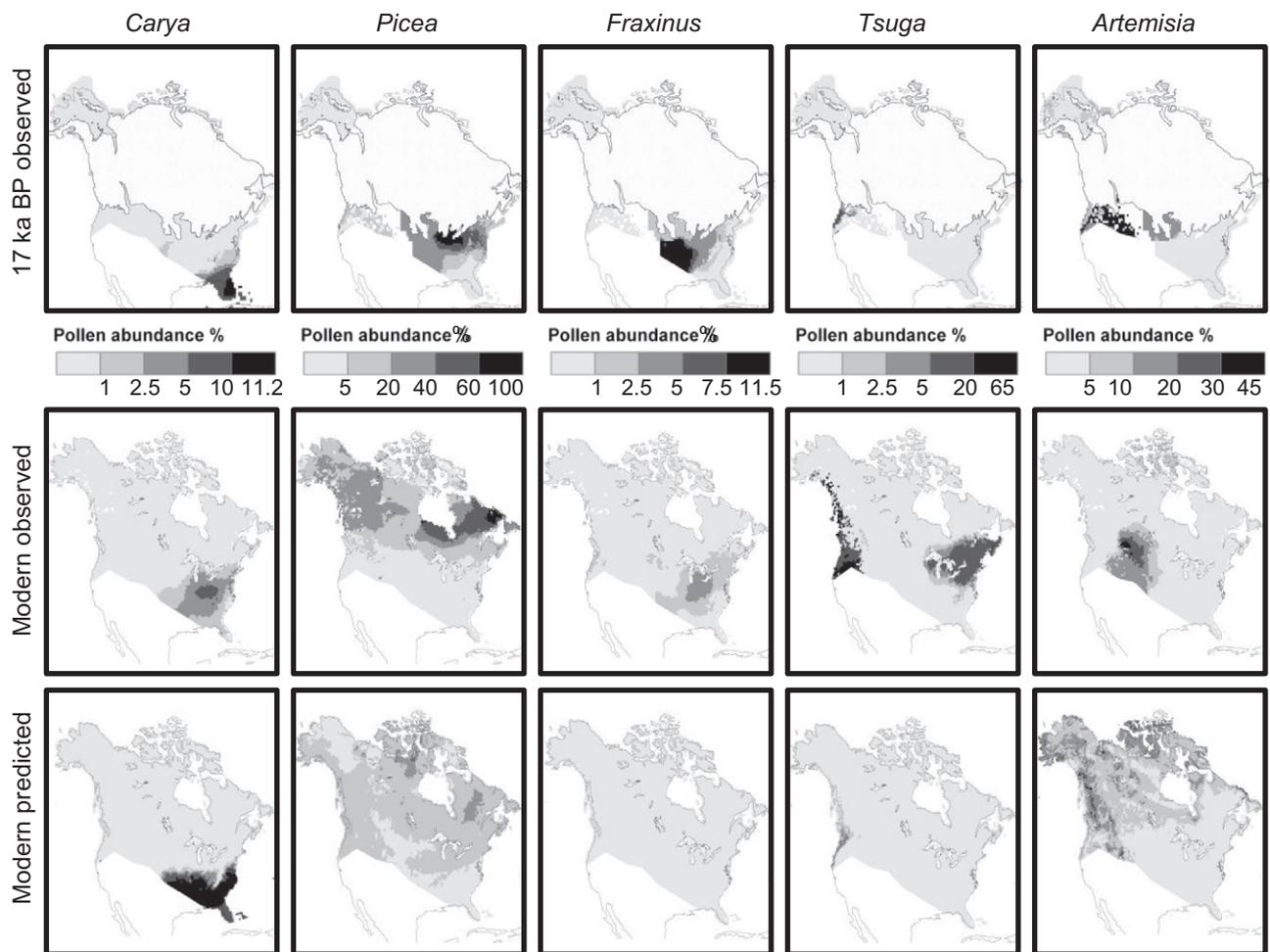


Figure 2 Observed and predicted distributions (17 ka BP, observed; 0 ka BP, observed and predicted) for five plant genera: *Carya* (hickory), *Picea* (spruce), *Fraxinus* (ash), *Tsuga* (hemlock) and *Artemisia* (sage). These distributions are based on species distribution models and data described here and by Veloz *et al.* (2012).

These climatic changes triggered large and well-documented shifts in species distributions (Williams *et al.*, 2004). The kinds of spatial responses differed among plant species, as does the predictive ability of SDMs (Fig. 2). Although the SDMs were consistently able to accurately predict the distribution of pollen abundances of the taxa modelled for the calibration period (21–15 ka) (mean cross-validated correlation between observed and predicted abundance = 0.77, SE = 0.03), these estimates of predictive accuracy do not always accurately reflect true predictive accuracy for the ‘future’ data (Veloz *et al.*, 2012). The pollen distributions of taxa such as *Carya* and *Picea* show strong evidence of a northward expansion, shifts that are reasonably well captured by the SDM. Other taxa, such as the eastern *Fraxinus* species, were more abundant in late-glacial records (primarily *Fraxinus nigra*) and less abundant today. Because the late-glacial pollen abundances of *Fraxinus* in eastern North America are highest in combinations of temperature and precipitation that no longer exist today (Williams & Jackson, 2007; Veloz *et al.*, 2012), the SDM incorrectly predicts very low *Fraxinus* abundances (< 1%) across eastern North America. Conversely, other

taxa, such as eastern *Tsuga* species and western *Fraxinus* species, were rare in the past and relatively common today. For these taxa, the SDM generally fails to predict their expansion. *Artemisia* shifts its range by less than predicted, presumably because the SDM underweights the importance of moisture availability on *Artemisia* distributions. The range of results shown in Fig. 2 illustrates the point that the predictive ability of SDMs varies among taxa, predictive ability being highest for relatively abundant taxa whose distributions are relatively temperature sensitive. Predictive ability is lower for taxa that are rare during the calibration period and for taxa that were abundant in past climates with no modern analogue.

Predicting ‘future’ reserve priorities

Abiotic strategy

Ranking reserves by solely maximizing their climatic dispersion under ‘future’ climates, with no information about ‘contemporary’ or ‘future’ species distributions, was an unsuccessful, even

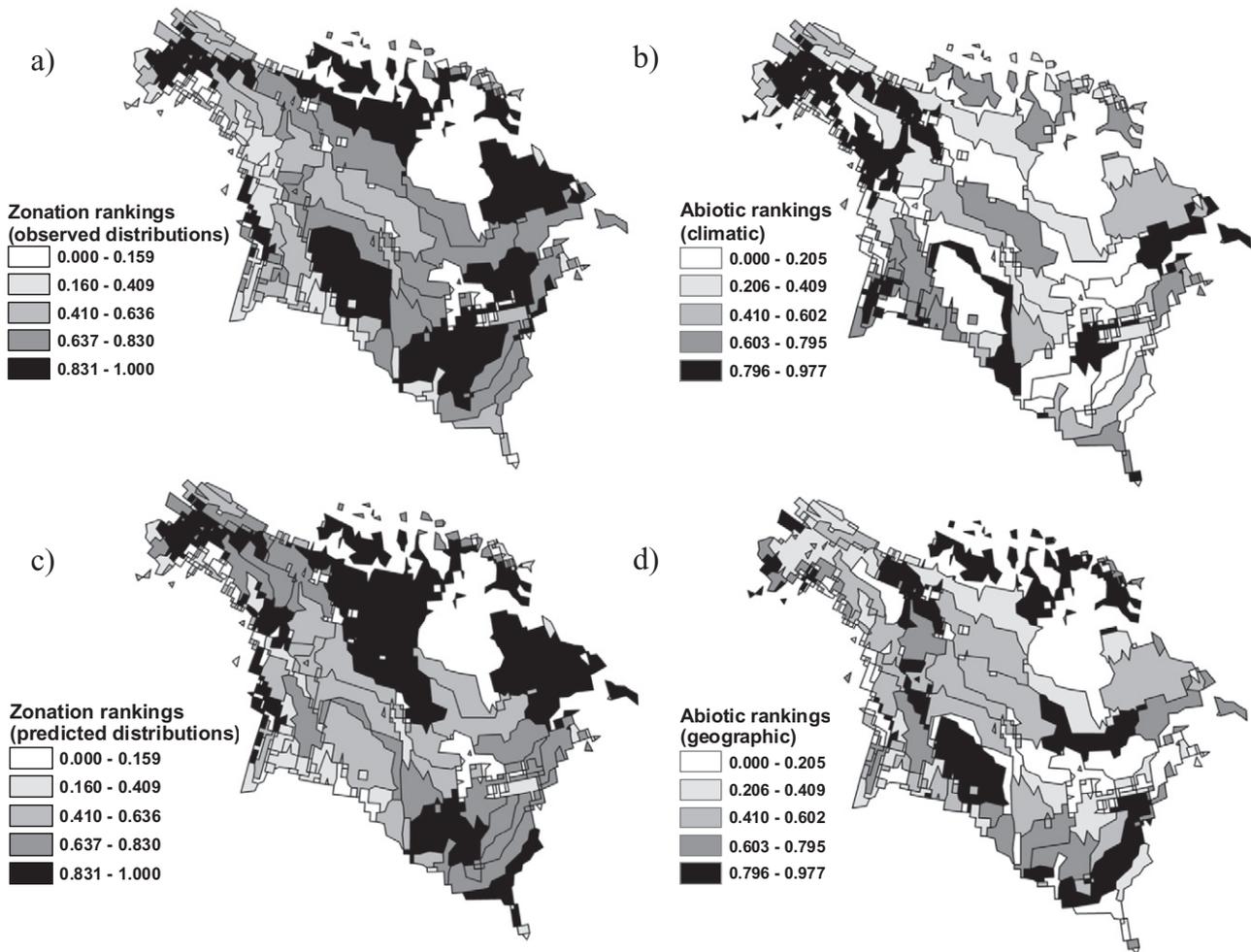


Figure 3 Maps showing the ranking of ecoregions based on (a) ZONATION applied to actual modern pollen abundances (the validation dataset) and (b)–(d) three set of predicted rankings by the ice age ecologist: (b) an abiotic ranking based on climate variables, (c) a SDM-based ranking based on ‘future’ predicted distributions of plant taxa and (d) an abiotic ranking based on geographic variables. Ecoregion rankings are not area-corrected.

misleading, strategy. When projected ‘future’ climates are used as the basis of the abiotic dispersion strategy, the IAE’s rankings are significantly but *negatively* correlated to the actual ZONATION ranking of modern reserves ($r = -0.260$, $P = 0.014$). These negative correlations occur because the abiotic rankings prioritize climatically dispersed ecoregions (Fig. 3b) and undervalue species-rich but climatically similar ecoregions (Fig. 3a). Thus, the climatic abiotic strategy is systematically incorrect. Similarly, there is no significant correlation between the abiotic ranking of ecoregions based on geographic redundancy and the actual ZONATION rankings ($r = 0.098$, $P = 0.364$, Fig. 3d). These results are qualitatively unaffected by adjusting for area effects (Table 2).

SDM strategy

Ranking reserves based on the ‘future’ predictions of SDMs that were calibrated using the IAE’s ‘contemporary’ datasets was more successful. When ecoregions were used as the basic unit of analysis, and before correcting for area effects, there was a strong correlation ($r = 0.802$, $P < 0.001$; Fig. 3a,c) between the IAE’s

rankings and the ZONATION ranking based on observed data (Fig. 4a). However, there is a strong effect of ecoregion area on the ZONATION rankings (Fig. 5). Larger ecoregions are consistently prioritized for conservation, presumably because they are more likely to have higher environmental heterogeneity, more overlap with species ranges and higher species abundances. Removing this area effect results in a reduced but still significant correlation ($r = 0.474$, $P < 0.001$) between the SDM-based rankings of the IAE and that of the validation dataset (Fig. 4b).

If grid cells are used instead of ecoregions, predictive ability decreases for the SDM-based rankings of the IAE (Fig. 6). When the number of grid cells is roughly the same as the number of ecoregions (88), the correlation between the actual rankings and SDM-predicted rankings drops to 0.395 ($P < 0.001$) and drops further to 0.217 ($P = 0.062$) after correcting for area effects. This finding suggests that the IAE’s unrealistically good knowledge of ‘future’ ecoregion distributions substantially improves the predictions.

The predictive ability of the SDM-based rankings drops further when grid cell size decreases (Fig. 6, Table 2). This effect

Strategy	Analysis unit	No. of reserves	Raw correlation		Area-corrected correlation	
			<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Abiotic climate	Ecoregions	88	-0.260	0.014	-0.222	0.037
Abiotic geographic	Ecoregions	88	0.098	0.364	-0.036	0.739
SDM	Ecoregions	88	0.802	< 0.001	0.474	< 0.001
SDM	Grid Cells	51	0.375	0.007	0.258	0.066
SDM	Grid Cells	76	0.395	< 0.001	0.217	0.062
SDM	Grid Cells	113	0.187	0.048	0.096	0.312
SDM	Grid Cells	182	0.163	0.028	0.114	0.126

Table 2 Summary results for the abiotic and species distribution model (SDM) strategies.

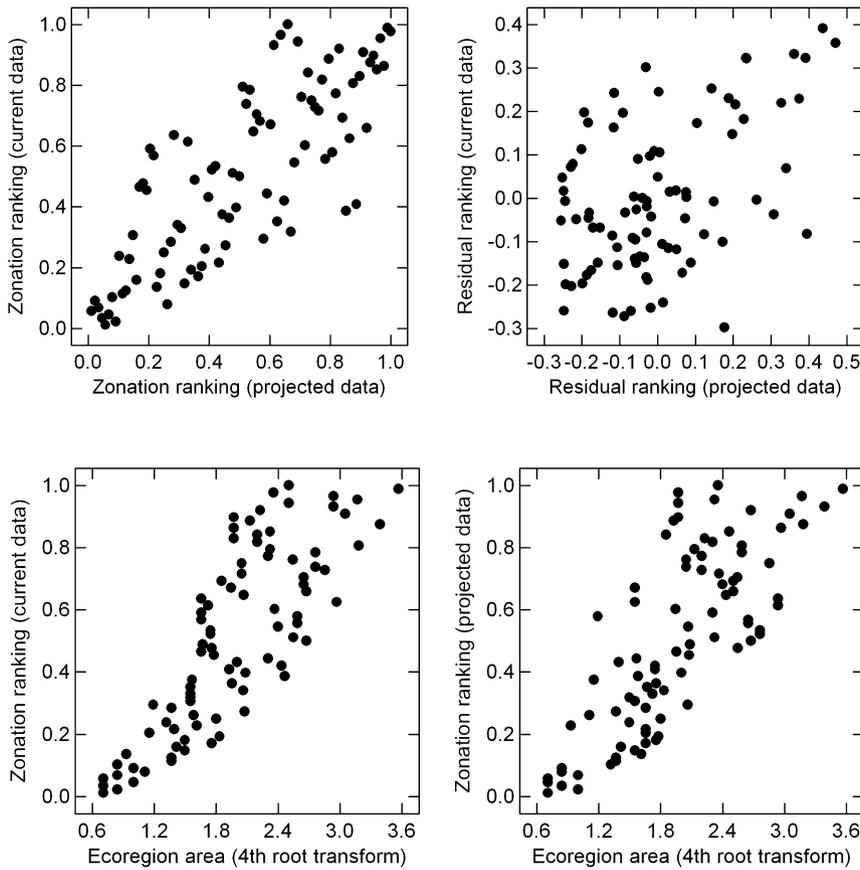


Figure 4 Scatter plots comparing the ZONATION ranking of ecoregions based on contemporary observed taxon distributions versus projected distributions for those same taxa: (a) raw ZONATION rankings; (b) ZONATION rankings for the residuals after area correction.

Figure 5 Scatter plots demonstrating the strong effect of ecoregion area upon the ZONATION rankings: (a) ZONATION ranking based on observed taxon distributions; (b) ZONATION ranking based on species distribution model projections.

is probably a consequence of the data used here, not an inherent limitation to ZONATION-based ranking approaches. When the number of taxa is small relative to the number of potential reserves, many grid cells have similar species composition and hence similar weights when determining rankings, causing the rank order of grid cells to be highly sensitive to even small changes in the input data.

Rank-and-regress strategy

Ranking reserves based on a regression analysis of ‘contemporary’ ZONATION rankings and climate variables is also moderately successful. The correlation between the predicted ZONATION ranking and modern observed ZONATION ranking ranges between 0.133 and 0.260 for grid cells when the original

weightings from the full-glacial multiple regression equation are used, and between 0.125 and 0.369 when all variables are weighted equally (all correlations corrected for area effects; Table 3). The *P*-values for these regression equations vary, but most are below the 0.05 threshold of significance. The smaller *P*-values and apparently higher significance associated with finer grid sizes is probably an artefact of the increasing number of grid cells in the gridded dataset.

DISCUSSION

The IAE’s objective – to protect future biodiversity by establishing a reserve network that will provide habitat for species after climate change has driven species range shifts – is shared by

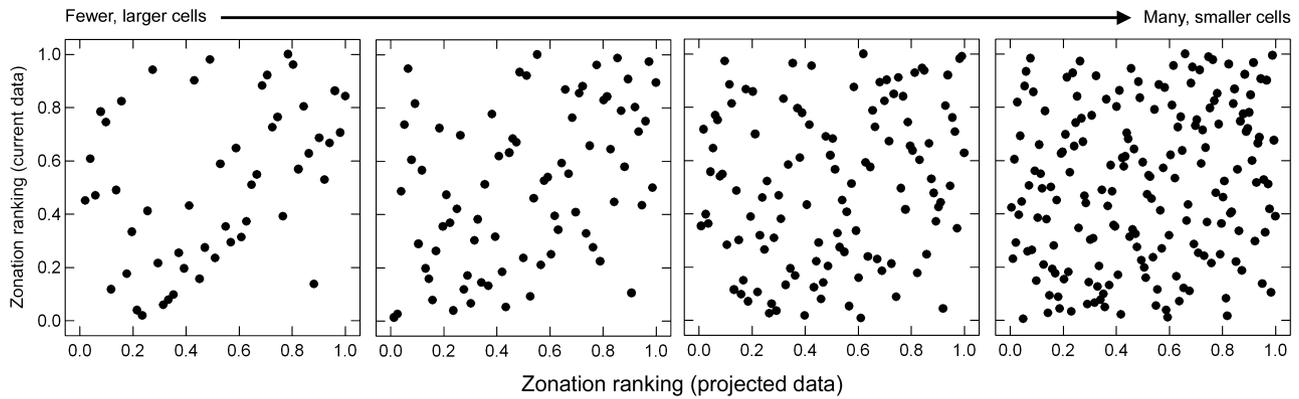


Figure 6 As in Fig. 4, these scatter plots compare the ZONATION rankings for actual species distributions versus rankings based on predicted distributions. Here the potential reserve units are grid cells instead of ecoregions. The grid resolution and number of grid cells increases from left to right.

Table 3 Summary results for the rank-and-regress strategy and its two variants in which (a) the weightings for predictor variables are based on stepwise regression or (b) predictors are weighted equally. All results have been corrected for area effects.

Grid resolution	No. of cells	Multiple regression prediction		Equally weighted predictors		Predictor variables*
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
Low	51	0.260	0.066	n.a.	n.a.	Standard deviation of DJF precipitation (+)
Medium-low	76	0.137	0.239	0.125	0.282	Within-season diurnal temperature range (BIO2) (–), standard deviation of elevation (–)
Medium-high	113	0.251	0.007	0.369	< 0.001	Within-season annual diurnal temperature range (BIO2) (–), mean DJF precipitation (+), standard deviation of elevation (–)
High	182	0.133	0.074	0.348	< 0.001	Precipitation seasonality (BIO15) (+), mean maximum daily spring temperature (–), mean autumn precipitation (+), mean minimum autumn temperature (+), mean elevation (+)

*+ or – signs indicate direction of correlation with ZONATION ranking. DJF, December, January, February.

modern conservation biologists. The datasets and tools available to the IAE are similar to tools widely used today to predict future species distributions and to develop climate-adaptation strategies. The challenges faced by the IAE (individualistic species responses, rare taxa with limited distributional data, incomplete overlap between ‘contemporary’ and ‘future’ climates) are also faced by efforts to predict ecological responses to 21st-century climate change. Given this, the limited success of the IAE’s efforts, as shown by the moderate to low correlations between predicted ‘future’ reserve rankings and actual reserve rankings, is cause for concern.

Some strategies are more successful than others. In particular, the abiotic strategy (Table 2, Fig. 3) – the only one to not use any information about the ‘contemporary’ distributions of species along climate gradients – performs poorly. This reinforces prior findings that environmental diversity is a poor indicator of biological diversity at continental scales (Araújo *et al.*, 2001). Moreover, the poor performance of the abiotic strategy relative to the IAE’s other strategies suggests that niche-based methods do add

value to the prioritization of reserves under climate-change scenarios, even if the distribution shifts for some taxa are poorly predicted (Fig. 2). The generally similar correlations reported for the SDM and reserve-and-rank approaches (Tables 2 & 3) indicate that the choice of method for incorporating empirical data on species–climate relationships does not greatly influence the IAE’s ability to predict reserve prioritization.

The IAE’s ability to use ‘contemporary’ species distributions and species–climate relationships to inform predictions of ‘future’ species distributions and reserve selection, albeit with only moderate success, is consistent with well-established findings that late Quaternary shifts in taxon abundances and distributions are linked to climate change (Wright *et al.*, 1993). For example, Prentice *et al.* (1991) showed that palaeoclimatic reconstructions based on one set of pollen taxa could accurately predict the late Quaternary distributions for other taxa ($r^2 > 0.60$ for all taxa), while Martínez-Meyer & Peterson (2006) showed that SDMs calibrated using full-glacial climate simulations and fossil pollen data could significantly predict modern distribu-

tions, and vice versa. These tests support assumptions that plant traits relevant to climate tolerance are conserved at millennial and shorter time-scales and that many plant species were able to shift their distributions quickly enough to track late Quaternary climate changes.

The more surprising finding is that the IAE's predictive ability is fairly low. One likely reason is that some late Pleistocene climates lacked modern analogues, allowing species to occupy portions of their fundamental niche that are currently unavailable (Williams & Jackson, 2007; Colwell & Rangel, 2009; Veloz *et al.*, 2012). Most hindcasting simulations for the late Quaternary have been run for the mid-Holocene (6 ka BP) and the Last Glacial Maximum (21 ka BP) (Nogués-Bravo, 2009). These time periods are traditionally popular for palaeoclimatic experiments because they represent earth system states suitable for testing the sensitivity of the climate system to altered insolation (6 ka BP) and large ice sheets and low greenhouse gases (21 ka BP) (Kutzbach & Guetter, 1986). Between these times, however, there was a period during the glacial–interglacial transition (roughly 17–12 ka BP) when insolation, atmospheric greenhouse gases and ice extent were all in different states from present and the earth system was transitioning between its glacial and interglacial states. This resulted in the emergence of climates with no modern analogue in portions of North America (Williams & Jackson, 2007) and reshufflings of plant taxa into new communities as species responded individually to climate change. By using a calibration dataset for the IAE that spanned 21–15 ka BP, we included data from these no-analogue communities and climates.

Recent analyses (Veloz *et al.*, 2012) suggest that the realized climatic distributions for some plant taxa in these no-analogue communities may have changed relative to the present. These changes are strongest for taxa such as *Fraxinus*, *Ostrya/Carpinus* and *Ulmus* that were abundant in the no-analogue communities and climates that prevailed in interior eastern North America during the late glacial period (Williams & Jackson, 2007; Veloz *et al.*, 2012). Thus, a key factor appears to be shifts in the realized niches of some species as they exploited climates that no longer exist at present. Additionally, lower-than-present CO₂ probably altered water–climate relationships for plants (Crucifix *et al.*, 2005), and the presence of diverse guilds of megaherbivores may have acted to suppress some taxa (Gill *et al.*, 2009). Others have noted apparent shifts in realized niches for some European tree taxa, with strong light-competitors showing smaller shifts (Pearman *et al.*, 2008). Given this evidence for shifting climatic distributions, it is unsurprising that models based upon assumptions of stable ecological niches would produce inaccurate predictions for some taxa and reduce the accuracy of predicted reserve prioritizations.

Migration lags probably limited the rates of post-glacial colonization for some taxa (Svenning & Skov, 2007; Araújo *et al.*, 2008), but lags do not seem to be the major factor in the data–model mismatches (Fig. 2) for the taxa studied here. First, some taxa such as *Picea* and *Carya* show large range shifts yet good agreement in overall distribution between the modern observed

and predicted distributions (Fig. 2), with no apparent sign that dispersal limitation is constraining their modern ranges. Second, post-glacial dispersal limitation should cause SDM-simulated modern ranges to be larger than observed distributions, yet the reverse is often seen here. For the taxa abundant in the late-glacial no-analogue communities, their modern abundance is underpredicted, suggesting that the model underestimates their ability to survive the disappearance of their late-glacial climates (e.g. *Fraxinus*, Fig 2). Similarly *Tsuga* (Fig. 2), is more widespread today than predicted, suggesting that this data–model disparity is due to the rarity of *Tsuga* in eastern North America between 15 and 21 ka BP, which provided insufficient calibration data to predict its post-glacial expansion.

This paper has focused on plant taxa and fossil pollen data, but virtually all biodiversity losses during the Pleistocene–Holocene transition were experienced by large vertebrates (Koch & Barnosky, 2006). So an interesting question for future work is whether current tools could have helped the IAE predict the megafaunal extinctions and the differential biodiversity impacts experienced by different taxonomic groups (Nogués-Bravo *et al.*, 2009).

Of course, for any given species, fossil-based distributional data are usually sparser than information based on modern observations, and are influenced by taphonomic processes that can blur their ecological signal. But does this mean that the IAE's experience is irrelevant? No, for several reasons. First, the species of most concern to modern conservationists are usually the rarest and most endemic taxa, which have the poorest distributional data. Conversely, the taxa analysed here are relatively abundant and well-represented in fossil records, and so arguably the IAE has as good or better distributional data for these taxa than are available for many threatened species. Second, we have given the IAE the advantage of working with distributional data from multiple time periods (i.e. 21–15 ka BP) and hence multiple states of the climate system. This provides a more robust description of species fundamental niches (Nogués-Bravo, 2009), which is just beginning to become available to modern ecologists from long-term and resurveyed data on species distributions (Moritz *et al.*, 2008). Lastly, as noted above, the information available to the IAE about the physical drivers of the 'future' climate system (Table 1) is far more precise than anything available to anyone engaged in conservation planning for the 21st century. So the IAE arguably has an easier challenge than ecologists working to conserve biodiversity in the face of global changes.

The IAE might have better success if more mechanistic models were employed, because process-based models should be relatively robust to novel environmental states (Buckley *et al.*, 2010). Dynamic vegetation models have been used to simulate transient vegetation responses to changing climate, soil conditions and atmospheric CO₂ over the late Quaternary, both for plant functional types and for individual species (Ni *et al.*, 2006; Giesecke *et al.*, 2010; Henne *et al.*, 2011). Other groups are using mechanistic energy-balance models of animal physiology to predict future species ranges (Kearney & Porter, 2009).

Correlative niche models nevertheless remain widely used by ecologists seeking to design reserve networks (Hannah *et al.*, 2007; Heller & Zavaleta, 2009) because of their operational advantages. Their simple data requirements makes it possible to run high-volume modelling exercises (e.g. Engler *et al.*, 2011), and they can be run for poorly studied species with distributional data but little information about their physiological requirements. These practical advantages are substantial, and we do not argue that correlative models should be discontinued. This analysis, however, reinforces the point that species may behave in unexpected ways when climate changes open up portions of the available environmental space (Jackson & Overpeck, 2000), as is expected for many regions in this century (Williams & Jackson, 2007). Hence reserve networks designed to preserve future biodiversity that are based primarily on projecting the contemporary spatial correlations between species distributions and climates forward in time, must be treated with caution and viewed as at best a rough guide to areas of potential future conservation value.

CONCLUSIONS

The limited ability of the IAE to successfully prioritize reserves for the environmental changes accompanying the last deglaciation is sobering, given the similar challenges faced by modern ecologists. Although the IAE has some disadvantages relative to modern ecologists, due to uncertainties inherent in studying past environments, the IAE enjoys the huge advantage of having more precise knowledge about greenhouse gas trajectories and 'future' climates than is available to modern ecologists. Various mechanisms might explain the poor performance of the IAE's predictive models, but an overarching reason is that the reserve predictions used here are based on correlative niche-based models, which capture only a portion of the processes controlling species distributions. Specific factors include the existence of past climates with no modern analogue, the shifts in realized ecological niches during those past no-analogue climates and the altered species interactions that resulted from individualistic species responses and the no-analogue communities that emerged in response to past climates. Overall, the IAE's experience suggests that niche-based empirical models based on spatial datasets of contemporary species–climate relationships do add value to designing future reserve networks, but only to a fairly limited extent.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Additional details about the implementation of ranking strategies.

BIOSKETCH

J.W.W., J.M., M.V., S.V. and H.K. designed the study; H.K. and M.V. ran ZONATION and reserve-ranking analyses; S.V. assembled palaeoclimatic and palaeovegetation data layers and ran the species distribution models; Z.L., B.O.B. and F.H. ran the CCSM3 transient climate simulations; J.W.W. wrote the paper with input from all authors.

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