Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity

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ABSTRACT

Aim Theoretical work suggests that species' ecological niches should remain relatively constant over long-term ecological time periods, but empirical tests are few. We present longitudinal studies of 23 extant mammal species, modelling ecological niches and predicting geographical distributions reciprocally between the Last Glacial Maximum and present to test this evolutionary conservatism.

Location This study covered distributional shifts in mammal species across the lower 48 states of the United States.

Methods We used a machine-learning tool for modelling species' ecological niches, based on known occurrences and electronic maps summarizing ecological dimensions, to assess the ability of ecological niches as modelled in one time period to predict the geographical distribution of the species in another period, and vice versa.

Results High intertemporal predictivity between niche models and species' occurrences indicate that niche conservatism is widespread among the taxa studied, particularly when statistical power is considered as a reason for failure of reciprocal predictions. Niche projections to the present for 8 mammal taxa that became extinct at the end of the Pleistocene generally increased in area, and thus do not support the hypothesis of niche collapse as a major driving force in their extinction.

Main conclusions Ecological niches represent long-term stable constraints on the distributional potential of species; indeed, this study suggests that mammal species have tracked consistent climate profiles throughout the drastic climate change events that marked the end of the Pleistocene glaciations. Many current modelling efforts focusing on anticipating climate change effects on species' potential geographical distributions will be bolstered by this result — in essence, the first longitudinal demonstration of niche conservatism.

Keywords

Climate change modelling, ecological niche, extinction, GARP, geographical distribution, Pleistocene, mammals, North America.

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INTRODUCTION

Many recent studies, and in particular a recent special issue (*Climate Change and Conservation*) of this journal, have focused on modelling species' ecological requirements and projecting those requirements onto modelled future climate regimes to anticipate future potential geographical distributions (Carey & Brown, 1994; Huntley *et al.*, 1995; Johnston & Schmitz, 1997; Kadmon &

Heller, 1998; Price, 2000; Peterson *et al.*, 2001; Bakkenes *et al.*, 2002; Berry *et al.*, 2002; Erasmus *et al.*, 2002; Midgely *et al.*, 2002; Peterson *et al.*, 2002b; Pearson & Dawson, 2003; Peterson, 2003; Peterson & Shaw, 2003; Siqueira & Peterson, 2003), with a review forthcoming (Peterson *et al.* 2004, in press). These species-specific models are being developed in parallel with other modelling efforts that focus at the level of ecosystems in the face of climate change (Tian *et al.*, 1998; Schimel *et al.*, 2000; Shaver *et al.*, 2000;

Bachelet *et al.*, 2001; Cramer *et al.*, 2001; Melillo *et al.*, 2001). However, whereas the ecosystem models have seen some degree of testing and validation (Oreskes *et al.*, 1994; Rastetter, 1996; Tian *et al.*, 1999; White *et al.*, 1999), the species-level models have seen little or no direct testing.

The ecological niche of a species can be defined as the range of environmental and biotic conditions within which its populations can persist without immigration (Hutchinson, 1957). In the face of environmental change, then (a) niche evolution or (b) movement to track niches spatially, become the only alternatives to extinction (Graham *et al.*, 1996; Brown & Lomolino, 1998). Recent theoretical work (Bradshaw, 1991; Brown & Pavlovic, 1992; Kawecki & Stearns, 1993; Kawecki, 1995; Holt & Gomulkiewicz, 1996; Holt, 1996) and empirical comparisons of niche characteristics between sister species (Huntley *et al.*, 1989; Ricklefs & Latham, 1992; Peterson *et al.*, 1999) suggest that ecological niches tend to remain relatively constant over evolutionary timescales and across space. However, recent experimental work argues that shifting interactions among species changes species distributional patterns so much as to make niche conservatism a moot point (Davis *et al.*, 1998).

Species' responses to global climate change provide a direct test of these hypotheses of niche conservatism. Both in past (Lanner & van Devender, 1981; Thompson & Mead, 1982; Wells, 1983) and ongoing (Parmesan, 1996; Parmesan *et al.*, 1999; Walther *et al.*, 2002; Parmesan & Yohe, 2003) climate change events, shifts in geographical distributions of species have been observed. Particularly dramatic climate change occurred since the Last Glacial Maximum (*c.* 18 000 years before present (year BP)), with numerous species moving tens of kilometres as climates warmed (Thompson & Mead, 1982; Wells, 1983; Lyons, 2003). The degree to which these shifts follow consistent climate regimes ('ecological niches', at least at coarse scales), however, has yet to be tested rigorously (Davis & Shaw, 2001).

Herein, we provide such a test. We use models of ecological niches to predict geographical distributions across this period of change for 23 extant mammal species to test long-term stability of ecological niches. This test is increasingly relevant in view of ongoing climate change events, with ecological niches as long-term stable constraints on geographical distributions, ongoing distributional shifts could be predicted and anticipated. We also apply this approach to eight taxa of mammals that went extinct at the close of the Pleistocene to assess the viability of climate-driven reduction of habitable area as an explanation for their extinction (Martin & Klein, 1984).

MATERIALS AND METHODS

Our analyses involve three steps: (a) modelling ecological niches for a single time period based on two climatic parameters (temperature and precipitation) and known occurrences of the species; (b) projecting the niche models onto modelled climates for a second time period; and (c) testing the ability of these models to predict known occurrences in the second time period. Tests are repeated reversing predictor and predicted time periods.

Input data

Ecological niches of mammalian species were modelled in the conterminous United States. Species were selected for analyses based on the number of record localities available in both the present and the Pleistocene (Last Full Glacial period, 14 500–20 500 year BP). We analysed only those species for which ≥ 5 unique localities (i.e. with geographical coordinates differing by > 3′) were available for both time periods, since sensitivity tests to sample size indicated that 5 unique localities was the minimum number to obtain significant predictions (see the 'Testing model predictions' section). A total of 23 extant and 8 extinct taxa (Pleistocene only) fit these criteria (Table 1), and all were included in our analysis; all species had reasonably large distributional areas in both time periods, on the order of one-fourth to one-half of the lower 48 United States. Species' occurrences for the present were obtained from the University of Kansas Natural History Museum (KUNHM) and Museum of Vertebrate Zoology, University of California, Berkeley (MVZ) via *The Species Analyst* distributed biodiversity database facility (*http://speciesanalyst.net*). Localities for the Pleistocene were obtained from the FAUNMAP

Table 1 Mammalian taxa used in the analyses. Extinct taxa are in bold type

Order	Family	Species
Insectivora	Soricidae	*Cryptotis parva*
		Notiosorex crawfordi
	Talpidae	*Scalopus aquaticus*
Chiroptera	Vespertilionidae	*Eptesicus fuscus*
Lagomorpha	Ochotonidae	*Ochotona princeps*
Rodentia	Sciuridae	*Tamias striatus*
		Spermophilus tridecemlineatus
	Castoridae	*Castor canadensis*
	Geomyidae	*Geomys bursarius*
	Muridae	*Microtus pennsylvanicus*
		Onychomys leucogaster
		Ondatra zibethicus
		Phenacomys intermedius
		Synaptomys cooperi
	Erethizontidae	*Erethizon dorsatum*
Carnivora	Canidae	*Canis latrans*
		Urocyon cinereoargenteus
		Canis dirus
	Ursidae	*Ursus americanus*
	Procyonidae	*Procyon lotor*
	Mustelidae	*Mephitis mephitis*
		Mustela frenata
	Felidae	*Lynx rufus*
Proboscidea	Elephantidae	***Mammut americanum***
		Mammuthus columbi
Perissodactyla	Equidae	***Equus conversidens***
Artiodactyla	Tayassuidae	***Platygonus compressus***
	Camelidae	***Camelops hesternus***
	Bovidae	***Bison bison antiquus***
		Oreamnos harringtoni
	Cervidae	*Odocoileus virginianus*

research database, a subset of the full FAUNMAP database, in which taxonomy and dating are standardized (FAUNMAP, 1994).

Climatic maps for the Pleistocene and present (mean annual temperature and mean annual precipitation; http://research. esd.ornl.gov/~hnw/valdai/) were used as the contextual information with which to generate ecological niche models; another four maps (potential vegetation, elevation, slope, aspect) were tested, but were eliminated from analysis owing to poor performance in predicting occurrences within time periods. Temperature and precipitation maps from the Pleistocene were estimated in a three-step process:

• an initial delta surface (Frenzel *et al.*, 1992) was interpolated using a regularized spline with tension and smoothing;
• obtaining a continuous map of current mean annual temperature and precipitation; and
• subtracting the delta surface from current temperature and precipitation maps to produce the final Pleistocene maps.

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.

Within GARP processes, first, a method is chosen from a set of possibilities (logistic regression, BIOCLIM rules, etc.), applied to the data, and a rule developed. Then, based on 1250 points resampled from the known occurrences and 1250 points sampled randomly from the study region as a whole, 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. 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 the addition of rules has no appreciable effect on the accuracy measure (convergence).

Distributional predictions from GARP may often include areas not inhabited by the species, an effect of the modelling being focused on ecological niches and potential geographical distributions, instead of on actual geographical distributions. These commission (overprediction) errors may in some cases be reduced by the inclusion of additional ecological dimensions or may require consideration of historical factors that lead to the absence of species from habitable areas (Peterson *et al.*, 1999; Peterson & Vieglais, 2001; Peterson, 2004 (in press)).

Since GARP generates distributional predictions based on a random-walk exploration of solution space, and predictions vary somewhat from one run to the next, we generated 100–1000 models per species. The 10 'best' models (those falling in an optimal combination of omission and commission error measures) were selected from among these models (Anderson *et al.*, 2003); the sum of this 'best subset' of models was used as the single representative potential geographical prediction for the species.

Testing model predictions

To test predictivity 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 niche projection, and statistical significance evaluated with a binomial test. The same process was followed to evaluate predictivity from Pleistocene to present, but because numbers of occurrence points were considerably higher (17–230 localities per species), χ^2 goodness-of-fit tests were used.

Because sample sizes were small for Pleistocene populations in all cases (all $n < 8$ unique localities), it was necessary to develop an assessment of the statistical power associated with our tests of predictivity across time. More precisely, firstly, to what degree can statistically significant models be developed based on just 5–7 input points (predictions Pleistocene to present), and secondly, to what degree can statistical significance be tested adequately based on 5–7 test points (predictions present to Pleistocene)? To this end, we used random subsets of the more abundant Recent occurrence data for each species in a paired suite of tests, as follows. For each species, for the first question, we used 100 randomly selected sets of 5 points to develop models, testing the statistical significance of each using the points not used for model-building. For the second question, for each species, we used 100 sets of all points available for the species except a randomly selected 5 to develop 100 models, and tested the statistical significance of each using the 5 points not used for model-building. These exploratory tests of sensitivity to low sample sizes (either for model building or for model testing), expressed as the percent of the 100 replicates developed showing strong statistical significance, permit us to assess how likely a negative result in the intertemporal comparisons is a result of sampling problems.

RESULTS AND DISCUSSION

An example result is that for the eastern mole (*Scalopus aquaticus*) (Fig. 1). As a test of model adequacy, predictions of the distribution of this species within time periods were highly statistically significant (present niche model predicts present distribution, $\chi^2 = 154.2$, d.f. = 1, $P < 0.001$; Pleistocene niche model predicts Pleistocene distribution, binomial test, $n = 5$, $P < 0.001$). Projecting the present niche model back to Pleistocene climatic conditions accurately predicted the known Pleistocene distribution of the species: i.e. coincidence between Pleistocene occurrence points and the back-projection of the present model was significantly higher than expected by chance (binomial test, $n = 5$, $P = 0.001$). Similarly, forward-projection of the Pleistocene model onto present climates was also highly statistically significantly coincident with present occurrence points ($\chi^2 = 61.62$, d.f. = 1, $P < 0.001$). Hence, the eastern mole followed a particular and predictable climate regime in its range shifts at the end of the Pleistocene.
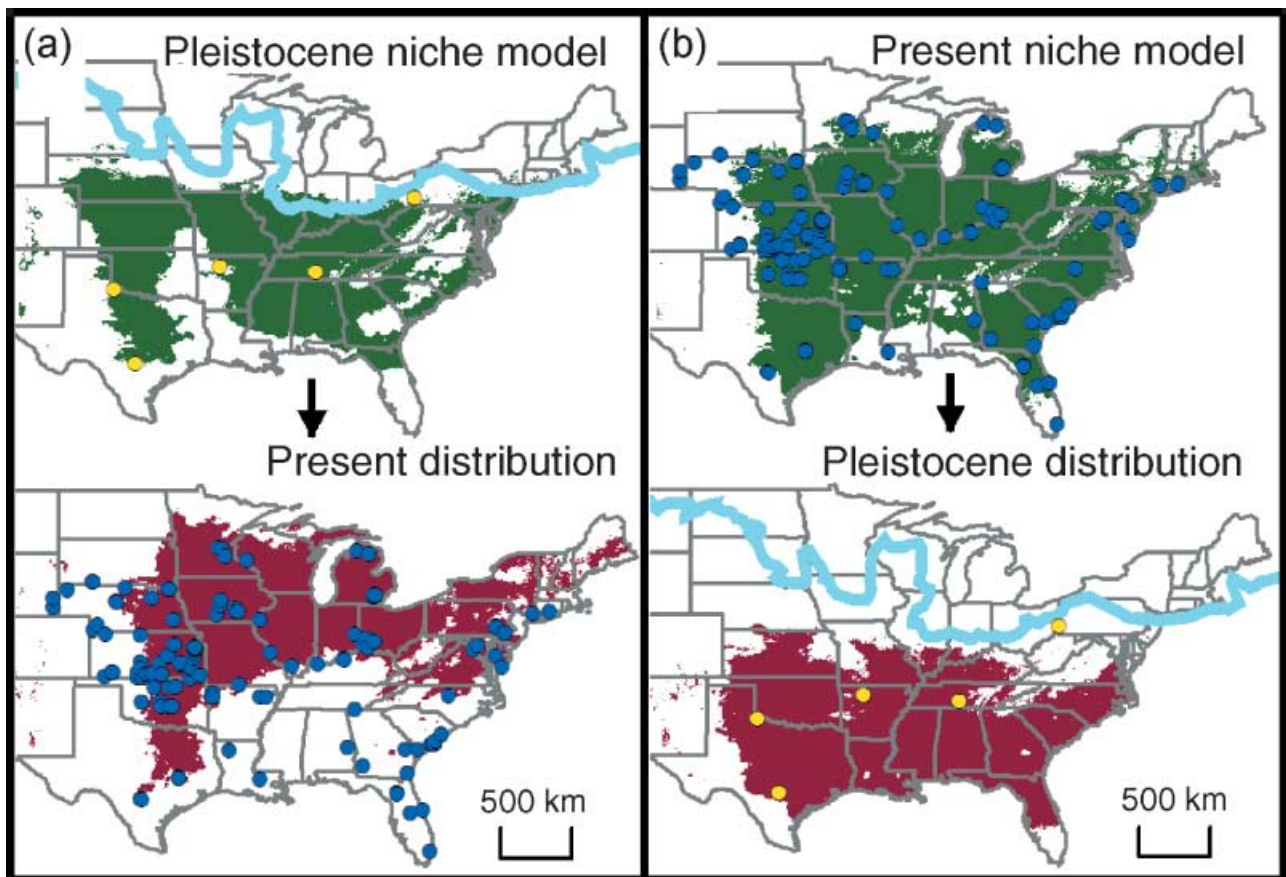
Figure 1 Inter-temporal predictions for the eastern mole (*Scalopus aquaticus*) for which predictivity between time periods was statistically significant ($P \geq 0.001$). (a) Niche model and prediction for the Pleistocene (top) and its projection to present climatic conditions (bottom). (b) Niche model and prediction for the present (top) and its projection to the Pleistocene climatic conditions (bottom). Yellow and blue dots are known occurrences in the Pleistocene and present, respectively. The blue line in the Pleistocene maps represents the ice sheet boundaries 18 000 year BP.

For the suite of 23 extant species analysed, all models were statistically significant within time periods (present, all $P < 0.001$; Pleistocene, all $P < 0.01$). Predictions between time periods were frequently statistically significant (Fig. 2): predictions for 9 species (*Notiosorex crawfordi*, *Scalopus aquaticus*, *Tamias striatus*, *Geomys bursarius*, *Microtus pennsylvanicus*, *Synaptomys cooperi*, *Urocyon cinereoargenteus*, *Mephitis mephitis*, *Odocoileus virginianus*) were significant both for Pleistocene predicting present and vice versa ($P < 0.05$); another 3 (*Cryptotis parva*, *Phenacomys intermedius*, *Procyon lotor*) were significant in predictions for Pleistocene to the present ($P < 0.05$) and marginally significant in predictions for present to Pleistocene ($0.09 > P > 0.05$). Six species' models (*Eptesicus fuscus*, *Spermophilus tridecemlineatus*, *Onychomys leucogaster*, *Ondatra zibethicus*, *Erethizon dorsatum*, *Mustela frenata*) were significant in predictions for Pleistocene to present ($P < 0.05$), but not in the other direction ($P > 0.1$); models for the remaining 5 species (*Ochotona princeps*, *Castor canadensis*, *Canis latrans*, *Ursus americanus*, *Lynx rufus*) were not significant in either direction ($P > 0.05$).

Particularly interesting are the results obtained for the heather vole (*Phenacomys intermedius*), for which a substantial range shift between time periods is deduced by the fossil and current localities. For this species, the prediction from Pleistocene to the present was statistically significant ($\chi^2 = 6.15$, d.f. $= 1$, $P = 0.013$), and marginally significant in the opposite direction (binomial test, $n = 6$, $P = 0.085$; Fig. 3).

Tests of sensitivity to small sample size indicated that for those species for which significantly predictive models could be developed, or for which powerful tests of significance could be developed, all were significant in intertemporal predictions. In particular, for tests of ability to develop significantly predictive models based on just 5 input points, species varied between 14–96% of 100 replicate models significant. The 9 species with > 76% of models significant were all highly significantly predictive Pleistocene to Recent ($P < 10^{-5}$), and the 14 species with > 65% of models significant were all significant or marginally significant ($P < 0.06$). The former result (the most significant 9 of 23 species all being statistically significant in predictions among time periods) was close to statistical significance in differing from random patterns ($P = 0.059$). Conversely, for tests of ability to *test* model significance powerfully based on just 5 test points, species varied between 5–100% of 100 replicate models significant. The 4 species with >
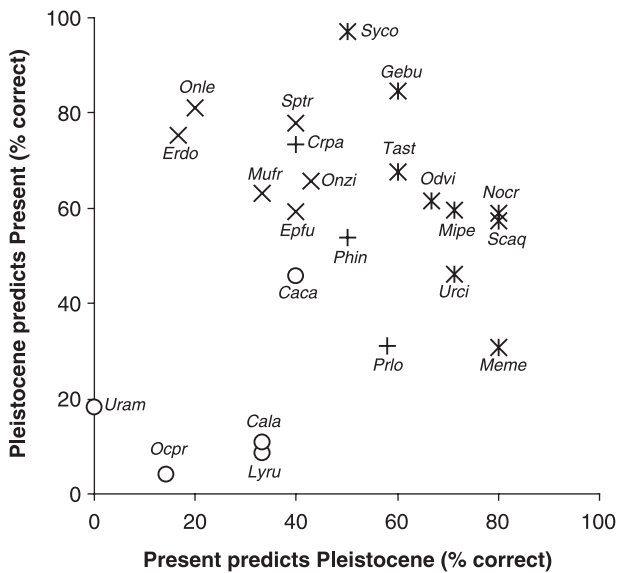
Figure 2 Relationship of percent predictivity of niche models in reciprocal intertemporal predictions (predictions of present distributions from Pleistocene models and Pleistocene distributions from present models). ⁎ represent species for which intertemporal predictions were statistically significant ($P < 0.05$) in both directions. + species that predicted statistically significantly for Pleistocene to the present ($P < 0.05$) and marginally significant in predictions for present to Pleistocene ($0.09 > P > 0.05$); × species significant in predictions for Pleistocene to present ($P < 0.05$) but not in the other direction ($P > 0.1$); ○ species not significant in either direction ($P > 0.05$). Abbreviations are as follows: *Caca, Castor canadensis*; *Cala, Canis latrans*; *Crpa, Cryptotis parva*; *Epfu, Eptesicus fuscus*; *Gebu, Geomys bursarius*; *Lyru, Lynx rufus; Meme, Mephitis mephitis*; *Mipe, Microtus pennsylvanicus*; *Mufr, Mustela frenata*; *Nocr, Notiosorex crawfordi*; *Ocpr, Ochotona princeps*; *Odvi, Odocoileus virginianus*; *Onle, Onychomys leucogaster*; *Onzi, Ondatra zibethicus*; *Phin, Phenacomys intermedius*; *Prlo, Procyon lotor; Scaq, Scalopus aquaticus*; *Sptr, Spermophilus tridecemlineatus*; *Syco, Synaptomys cooperi*; *Tast, Tamias striatus*; *Uram, Ursus americanus*; *Urci, Urocyon cinereoargenteus*; *Erdo, Erethizon dorsatum.*

70% of models significant were all significantly predictive Recent to Pleistocene; the probability that none of the 14 nonsignificant species in the Recent to Pleistocene predictions would rank among the top 4 in significance when tests were based on 5 test points is low ($P = 0.014$). Hence, in both cases, those species for which sample sizes of $n = 5$ were sufficient either for model building or model testing were uniformly statistically significant in their predictions among time periods.

In general, potential distributional areas of species expanded at the end of the Pleistocene (13 species expanded, 7 equivocal, 3 contracted). The only species predicted to have contracted dramatically (74.6% reduction) is the pika (*Ochotona princeps*), a specialist of near-tundra talus slopes, which have become much less extensive in North America (Fig. 4). Lack of predictivity of distributions between time periods for this species makes this pattern difficult to interpret.

The results of this study thus indicate that many of the species tested have not changed in their ecological characteristics over the past 18 000 years. Those species for which intertemporal predictivity was not significant tended to be precisely those species for which models based on small sample sizes were generally not significant within time periods, or those for which model tests based on small sample sizes were not powerful within time periods. The idiosyncrasy of species ranges' shifts during the Pleistocene-Holocene transition (Graham *et al.*, 1996; Lyons, 2003), and the ability to predict them supports the hypothesis of niche conservatism over long-term ecological time periods. Moreover, by integrating the ecological niche modelling approach with quantitative evaluations of morphology and population trends of species in the face of previous climatic changes (Barnosky *et al.*, 2003), we see the potential for robust, spatially explicit predictive evaluations of populations and species to present ongoing warming episodes.

Still, not all species analysed showed predictivity between time periods. Two factors may be responsible: one methodological (sample sizes for building models and testing model predictions were very small in the Pleistocene samples), and the other biological (niche evolution or interspecific interactions). Pleistocene models projected to the present were generally much more predictive than present models projected to the Pleistocene: without exception, when predictivity was not significant in one direction, that direction was from present to Pleistocene, where sample sizes for testing were low (5–7 occurrence points). Previous such model tests have shown that small test sample sizes strongly affect ability to discern between good and bad models (Peterson *et al.*, 2002a), and indeed our tests of the adequacy of models or model tests based on 5 points suggest that these species would likely show intertemporal predictivity were sample size not a concern. Lack of significant intertemporal prediction in 5 species may result from sample-size complications (i.e. none of the 5 performed better than 76% in model building, or better than 45% in model testing, at small sample sizes).

Alternatively, however, the lack of predictive ability in these species may truly reflect evolutionary change in temperature-precipitation niches, or possibly rearrangements of interpecific interactions that permit or cause distributional shifts (Davis *et al.*, 1998). Four out of the 5 species that showed no significant intertemporal predictivity are currently widespread across the conterminous US (*Castor canadensis, Canis latrans, Ursus americanus*, and *Lynx rufus*); in general, widespread species performed worse than species with more restricted ranges. Species with extensive geographical ranges generally have broader climatic niches, so distributional restrictions may have more to do with factors not directly related to climate. For example, it is well documented that coyote (*Canis latrans*) abundance and distribution are limited by other predators, particularly the wolf (*Canis lupus*) (Dekker, 1989). In areas where wolf populations have been reduced or extirpated, coyote populations have increased and its distributional range has expanded (Sheldon, 1992). Considering that in the Pleistocene many more large mammals were present in this region than today, ecological interference might have been stronger among them, particularly among carnivores.
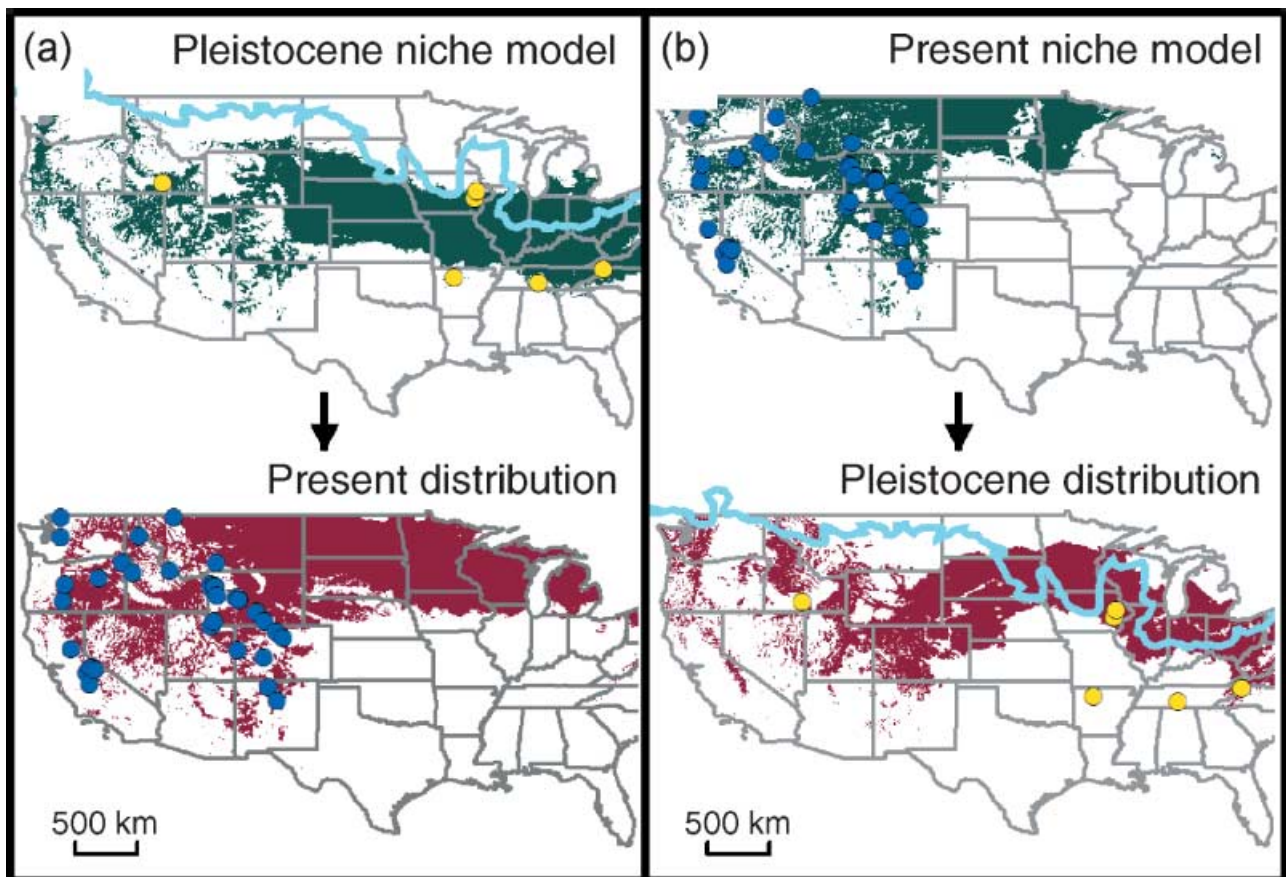
Figure 3 Inter-temporal predictions for the heather vole (*Phenacomys intermedius*) for which Pleistocene to the present predictivity was statistically significant (*P* = 0.013), and marginally significant in the opposite direction (*P* = 0.085). (a) Niche model and prediction for the Pleistocene (top) and its projection to present climatic conditions (bottom). (b) Niche model and prediction for the present (top) and its projection to the Pleistocene climatic conditions (bottom). Yellow and blue dots are known occurrences in the Pleistocene and present, respectively. The blue line in the Pleistocene maps represents the ice sheet boundaries 18 000 year BP.

Extinction of several large predators could conceivably have released surviving species from restrictive interactions and distributional changes might have been driven by their dispersal possibilities or other factors at the landscape level more than by climate.

Of particular interest in these considerations is the pika *Ochotona princeps*. In the sensitivity test to low sample size, this species was the 'best' performer both for building and for testing models. It also appears to have quite narrow and predictable ecological requirements; however, predictivity lacked statistical significance in both directions (Fig. 4). Further testing with improved sample sizes will be necessary to draw conclusions.

High predictivity of distributions from ecological characteristics in general, however, suggests that species follow stable climatic niches across space and through time. This result strengthens the conclusion that species' ecological niches represent long-term stable constraints on distributional possibilities; adaptation to novel environmental conditions, even when major climatic changes take place, appears rare. These results coincide with other recent studies that assessed niche similarity between allopatric sister species pairs (Huntley *et al.*, 1989; Ricklefs & Latham, 1992;

Peterson *et al.*, 1999), and provide the first longitudinal evidence of niche conservatism as a widespread pattern in the evolutionary and biogeographical history of species (Holt & Gaines, 1992; Kawecki, 1995; Holt & Gomulkiewicz, 1996). This result adds significantly to the case for ecological niche modelling as a viable approach to anticipating climate change effects on species' distributional potential (Pearson & Dawson, 2003).

Finally, previous discussions of causes of mammalian extinctions at the end of the Pleistocene have balanced human-mediated explanations (Martin, 1984; Alroy, 2001) against ecological explanations (e.g. habitable areas for species decreased or disappeared with climate change (Guilday, 1984; King & Saunders, 1984)). Of eight mammal taxa that went extinct at the end of the Pleistocene and for which sample sizes were sufficient, changes in size of potential distributions suggest that reduction of habitable area *per se* owing to climate change is not a sufficient explanation for their extinction. Indeed, only two species saw reductions in habitable areas (*Canis dirus*, 29.6%; *Camelops hesternus*, 16.6%), whereas the habitable area of the remaining six (*Mammut americanum*, *Mammuthus columbi*, *Equus conversidens*, *Platygonus compressus*, *Bison b. antiquus*, *Oreamnos harringtoni*) expanded
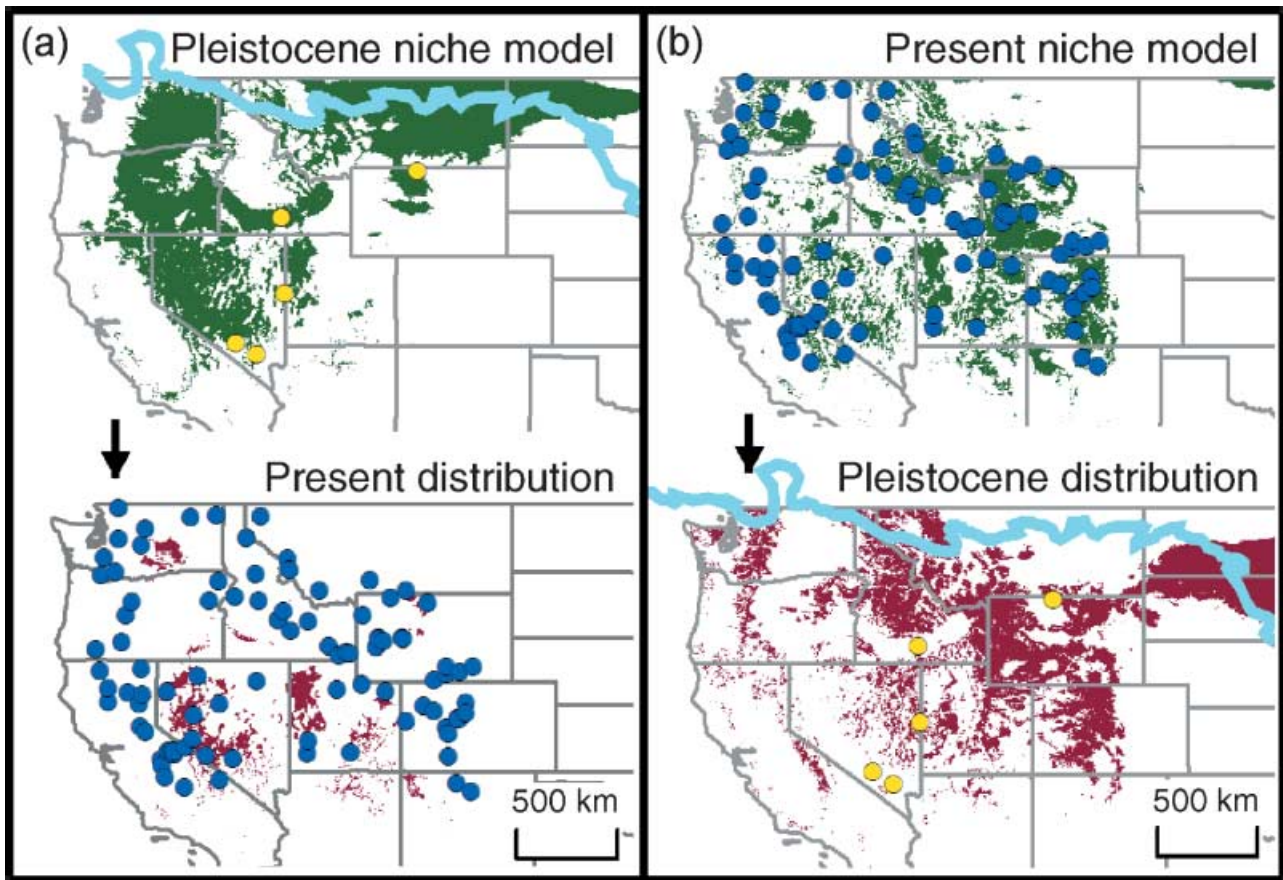
Figure 4 Inter-temporal predictions for the American pika (*Ochotona princeps*) for which predictivity between time periods was statistically nil (*P* > 0.05). (a) Niche model and prediction for the Pleistocene (top) and its projection to present climatic conditions (bottom). (b) Niche model and prediction for the present (top) and its projection to the Pleistocene climatic conditions (bottom). Yellow and blue dots are known occurrences in the Pleistocene and present, respectively. The blue line in the Pleistocene maps represents the ice sheet boundaries 18 000 year BP.
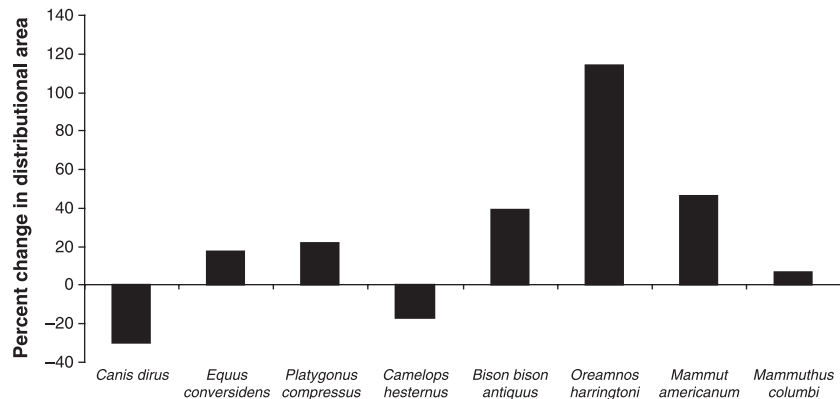

Figure 5 Predicted percent change of potential distributional area from the Pleistocene to the present for eight extinct Pleistocene mammal species.

by 6.9–114.0% (Fig. 5; average 41.0% increase). Sample size considerations concerning model-building based on small occurrence data sets certainly apply here, as none of the extinct species was represented by more than six occurrence points. Nevertheless, the broad-brush pattern of increasing potential range size over the end of the Pleistocene is likely to be robust, even if models are not completely adequate to represent the potential distribution of a particular species. Although other hypotheses of climate change as causal factors for the megafaunal extinction require further testing [e.g. changes in seasonality patterns and climatic minima and maxima; disruption of biotic interactions in the Pleistocene-Holocene transition; strong climate fluctuations within decadal to century scales (Slaughter, 1967; Graham & Lundelius, 1984; Guthrie, 1984; Kiltie, 1984; Dansgaard,

1993; Mayewski, 1993)], changes in mean climate values appear less likely to be responsible for these extinctions.

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BIOSKETCHES

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