

Quaternary Climate Change and the Geographic Ranges of Mammals

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ABSTRACT: A species' range can be a proxy for its ecological well-being. Species with small and shrinking range distributions are particularly vulnerable to extinction. Future climate change scenarios are predicted to affect species' geographical extents, but data on how species' distributions respond to changing climate are largely anecdotal, and our understanding of the determinants and limits to species' geographic ranges is surprisingly poor. Here we show that mammal species in more historically variable environments have larger geographical ranges. However, the relationship between range size and long-term climate trends cannot be explained by variation in our estimates of habitat specificity. We suggest that large oscillations in Quaternary temperatures may have shaped the contemporary distribution of range sizes via the selective extirpation of small-ranged species during glacial expansion and/or recolonization by good dispersers after glacial retreats. The effect of current climate change on species' distributions and extinctions may therefore be determined by the geographical coincidence between historical and future climate scenarios, the "mesh size" of the extinction/dispersal filter imposed by past climate change, and whether similar ecological and evolutionary responses to historical climatic change are appropriate in an increasingly transformed and fragmented landscape.

Keywords: Quaternary climate, sister contrasts, extinction filter, dispersal filter, habitat specificity, range size.

Introduction

A species' geographic range is one of the elemental units of biogeography (Rosenzweig 1995; Brown et al. 1996; Brown and Lomolino 1998). Species' geographic ranges vary in size, location, shape, connectedness, and occupancy (Brown et al. 1996; Gaston 2003). Among these variables, range size is perhaps the simplest yet least understood aspect of a species' distribution. Species' range limits will reflect the abiotic conditions that define their fundamental

niche. Constraints to niche evolution may limit the invasion of new habitats and climates, thereby restricting range extents (Wiens and Donoghue 2004). Across species, range size varies over several orders of magnitude (Brown et al. 1996; Sechrest 2003). Within terrestrial mammals for which we have distribution data, ranges vary in size from less than 10 km², (e.g., the Ryukyu mole *Mogera uchidai*, endemic to the largest of the Japanese Senkaku Islands) to tens of millions of square kilometers (e.g., the red fox *Vulpes vulpes*). Within species-rich clades, the frequency distribution of range sizes is typically right skewed, with most species having small to medium ranges (Brown et al. 1996). Species with large ranges drive regional and global patterns of species richness (Jetz and Rahbek 2002), whereas regions with high concentrations of species with restricted ranges are frequently targeted as conservation priorities (Myers et al. 2000; Brooks et al. 2006).

The erosion of species' ranges by habitat transformation and loss is currently the most important driver of mammalian extinctions (Schipper et al. 2008). Climate change is likely to be an increasingly important future threat (Millennium Ecosystem Assessment 2005) and perhaps the dominant driver of extinction risk within Arctic, alpine, and boreal ecosystems (Sala et al. 2000). Rising global temperatures are already thought to have affected current species' distributions (Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2006). Projected climate change scenarios predict a reduction in the size of suitable habitat within species' current climatic niches and, by extrapolation of species-area relationships (e.g., Thomas et al. 2004; Malcolm et al. 2006; Pimm et al. 2006; Jetz et al. 2007; Williams et al. 2007) or extinction-range size relationships (e.g., Thuiller et al. 2006; Lee and Jetz 2008; Şekercioglu et al. 2008), a cataclysmic loss of biodiversity. However, predicting the future distributions of species under climate change is difficult because we do not have information on future ranges with which to evaluate model accuracy (Araújo and Rahbek 2006; Lewis 2006; Davies et

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al. 2008). In addition, species' range adjustments are likely to be individualistic, conditional on the interaction between the biotic and abiotic environments, biological traits, and the evolutionary and climatic history of the region in which they occur (Hampe 2004; Thuiller et al. 2005; Heikkinen et al. 2006).

Here, we use differences between sister species to explore correlates of geographic range size in terrestrial mammals. Specifically, we evaluate the effect of Quaternary climate oscillations on contemporary mammalian geographic distributions. Large oscillations in Quaternary climate might have had a direct effect on the distribution of species' range sizes (fig. 1, path *a*) through the loss of small-ranged species (Brown 1995; Rohde 1996). Large range size might provide a buffer against extinction, for example, because large-ranged species may be more likely to occupy "refuge" habitats or are composed of a greater number of individuals, enabling survival and recolonization after localized extinction events (Gaston 2003). In addition, large-ranged species may be good survivors because they are inherently better at coping with a wider variety of environmental conditions (Stevens 1989; Owens and Bennett 2000; Fisher and Owens 2004). Even if extinction were random with respect to range size, species might still tend to have greater range extents where Quaternary climate oscillations have been most pronounced if recolonization after glacial retreats favored good dispersers and hence species predisposed to broad geographic ranges (Price et al. 1997). Alternatively, large oscillations in Quaternary climate may have favored large-ranged species via selection for habitat generalists (fig. 1, path *b-c*) capable of occupying a broad spectrum of habitat types (Brown 1995; Rohde 1996; Rohde and Heap 1996).

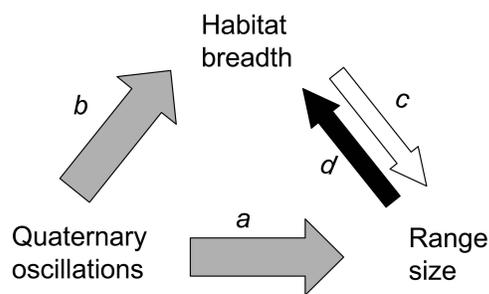


Figure 1: Alternate pathways linking climate change with species' habitat breadth and geographic range. Path *a*, direct effect of Quaternary climate oscillations on range size via either extinction of small-ranged species or selective recolonization by good dispersers. Path *b-c*, indirect effect of Quaternary climate oscillations on species' range sizes via favoring species with broad environmental tolerances, hence capable of occupying a greater breadth of habitat types. Path *d*, reciprocal pathway linking environmental tolerance and geographic range; species with larger ranges might occupy a greater breadth of habitat types simply by chance.

Sister-species contrasts provide a statistically powerful approach for detecting significant associations between species' attributes that are under the influence of multiple variables and where some of those variables are phylogenetically conserved (Harvey and Pagel 1991), which is likely the case for range size and location. Understanding the determinants of geographic range size will be invaluable for effective conservation management because of the close correlation between the size of a species' geographic range and the risk of extinction (Purvis et al. 2000; Cardillo et al. 2005, 2008). By exploring species' responses to past climate change, we hope to provide a foundation for projecting forward to estimate the likely effect of current climate trends on species' distributions and extinctions.

Methods

Data

An overview of the geographic distribution of range sizes across terrestrial mammals was generated from the database of mammalian distributions collated by Sechrest (2003) and modified as described by Grenyer et al. (2006). All resolved sister-species pairs of terrestrial mammals ($n = 545$) were identified from the recently published species-level phylogenetic tree of mammals assembled by Bininda-Emonds et al. (2007). Species values for body mass, range area, temperature, and actual evapotranspiration (AET) were taken from the PanTHERIA database of mammal life histories and distribution (Jones et al., forthcoming). Underlying geographic information system (GIS) layers for temperature and AET were derived from remote sensing data at a resolution of $0.5^\circ \times 0.5^\circ$. Species values represent area-corrected means estimated as described by Davies et al. (2004). We also estimated one index of seasonality as the maximum difference in annual temperatures, from monthly means, averaged across cells within each species' range. Other environmental variables are also likely to vary seasonally, including precipitation, productivity, and temperature variability. We therefore included species' latitude, calculated as mean degrees from the equator using a $0.25^\circ \times 0.25^\circ$ grid, in the hope of capturing additional environmental parameters that covary with latitude, although it remains possible that other important variables were not included in our analysis. GIS coverages of change in temperature and change in precipitation since the last glacial maximum were estimated using the HadCM3M2 Ocean-Atmosphere-Vegetation experiment from the Paleoclimate Modelling Intercomparison Project Phase II (<http://pmip2.lsc.ipsl.fr/>; Braconnot et al. 2007); the "modern" climate was representative of preindustrial levels. This measure correlates closely with climatic oscil-

lations throughout the Quaternary (Jansson 2003). We used outputs from the HadCM3M2 model ($2.5^\circ \times 3.75^\circ$ resolution) because they spanned the time frame of interest (21,000 years ago to present) for both temperature and precipitation. Mean species values reflecting the magnitude of postglacial climate change in temperature (ΔT) and precipitation (ΔP) across a species' range were then estimated as above. Area and ΔT were log transformed before further analyses.

In addition, for each species, we calculated an index of dispersion (k) to quantify habitat specificity as

$$\frac{\bar{y}_i^2}{\text{Var}(y_i) - \bar{y}_i},$$

where y is the area of occupancy within each of the 15 terrestrial land cover classifications from the Simple Biosphere Model of the U.S. Geological Survey Global Land Cover Characterization database (<http://eros.usgs.gov/products/landcover/glcc.php>). Land cover classifications were based on core remote sensing data (Normalized Differential Vegetation Index) from the Advanced Very High Resolution Radiometer sensor on the National Oceanic and Atmospheric Administration series of polar-orbiting satellites (Sellers et al. 1986). Species with most of their range falling into a single land cover type (specialists) have low values of k , for example, Kloss's gibbon *Hylobates klossii* ($k = 0.07$) and the short-eared rock wallaby *Petrogale brachyotis* ($k = 0.08$); species more equally distributed across land cover types (generalists) have high values of k , for example, the hoary bat *Lasiurus cinereus* ($k = 1.20$) and the red fox *Vulpes vulpes* ($k = 1.04$).

Contrasts between sister species were then calculated for each variable as $X_A - X_B$, where X_A is the species value for sister A and X_B is the species value for sister B. The full list of sister pairs and the magnitude and direction of contrasts are provided in table A2 in the online edition of the *American Naturalist*.

It is likely that there is variation in how accurately contemporary species ranges capture the different environmental variables. GIS coverages derived from remote sensing data will be more precise than models reconstructing paleoclimates. However, species range maps also contain errors; in addition, species may not occupy the entire region within the bounds of their distribution (cf. area of occupancy and extent of occurrence), for example, because some habitats might be unsuitable (Brown et al. 1996). To explore model sensitivity, we therefore additionally extracted species values for each environmental variable from species range midpoints (see "Correlates of Range Size"). Although it is not immediately obvious to us how errors in our range data might generate false correlations, it is

possible that noise associated with measures for closely intercorrelated variables might result in unstable estimates of model coefficients, making it difficult to distinguish between predictor variables. We assessed potential for bias in two ways. First, we examined the correlation strength between each pair of predictor variables. Second, we estimated multicollinearity in our regression models by way of variance inflation factors (VIFs). For cases where collinearity was high, models were constructed that excluded each of the intercorrelated variables in turn. We assumed a VIF of 10 to be important (Belsley et al. 1980).

Statistical Analysis

We generated a series of regression models to explore the correlation between contrasts in range size, habitat specificity (k), and various environmental parameters, including the magnitude of postglacial climate change. All analyses were performed in the statistical package R (R: a programming environment for data analysis and graphics, ver. 2.4.0; <http://www.r-project.org>), using regression through the origin on sister-species contrasts (Harvey and Pagel 1991). For some species, particularly island species, it is likely that hard boundaries constrain the realized range size. It is also likely that some species have undergone recent range contractions because of anthropogenic influences, for example, habitat alteration (Ceballos and Ehrlich 2002). We therefore present model coefficients excluding island endemics and species classified as threatened by the International Union for Conservation of Nature (IUCN) Species Survival Commission (IUCN Red List of Threatened Species; <http://www.iucnredlist.org/>), giving a sample size of 296 sister pairs (592 species). We explored model sensitivity by relaxing these constraints and repeating the analyses including all sister species in the start models ($n = 545$ pairs). We did not extend this analysis to include nodes deeper in the phylogenetic tree because this would have required additional assumptions regarding the mode of inheritance and evolution of geographic range, for which justification is weak (Losos and Glor 2003; Waldron 2007).

First, we regressed contrasts in range size against each environmental variable in turn to summarize the general relationship between range size and the various predictor variables. Second, we constructed maximal models with range area as the response variable and temperature, AET, latitude, seasonality (mean annual change in temperature between the hottest and the coldest months), ΔP , ΔT , and body mass as explanatory variables. We then performed model simplification by removing nonsignificant terms ($\alpha = 0.05$) from the maximal models (Crawley 2002). If climatic variability favored habitat generalists and generalists were in turn able to occupy larger geographic ranges

(fig. 1, path *b-c*), we would predict climate variability to be dropped from the minimum adequate model, because habitat specificity would be the more immediate predictor of range size (fig. 1, path *c*). Conversely, if climatic variability favored species with large geographic ranges irrespective of habitat specificity (fig. 1, path *a*), for example, because small range size is associated with fewer individuals and hence increased sensitivity to demographic perturbations, we would predict *k* to be dropped from the minimum adequate models.

To explore whether the determinants of species range size differ between regions known to vary in their climatic histories, we ranked species by the maximum value of ΔT across their ranges and then compared models fitted to sister species within the upper third (experiencing large changes in temperature since the last glacial maximum) with those fitted to sisters within the lower third (experiencing small changes in temperature since the last glacial maximum). We note that sister species falling within the upper third are largely restricted to high northern latitudes, because glacial oscillations have been most pronounced in this region.

Continent shape might also be an important constraint on the potential range size a species can obtain. For example, in the Southern Hemisphere “continental drip” (Holden 1976) reduces continental land surface area toward the pole. We therefore repeated the set of regression models, using the proportion of available land area occupied (occupancy), rather than absolute area, as the response variable. Occupancy was estimated as the geographic area covered by land contiguous with a species’ distribution (i.e., not separated by sea) within the latitudinal extents of the species’ range (Waldron 2007). Because our measure of occupancy was bounded between 0 and 1, it was arcsine transformed before subsequent analysis. Our index of occupancy assumes that species’ ranges are constrained latitudinally, for example, because of environmental tolerances, but not longitudinally. An alternative approach would be to construct a bioclimatic envelope for each species and to estimate relative occupancy of suitable habitat (e.g., see Letcher et al. 1994). However, the accuracy of bioclimatic models hinges on the questionable assumption that species are in equilibrium with the contemporary environment (Araújo and Rahbek 2006). In addition, defining appropriate limits to the envelope is highly subjective and at one extreme will delimit only the area in which the species is actually present (Brown et al. 1996).

Finally, we evaluated the relationship between habitat specificity (*k*) and Quaternary climate change (fig. 1, path *b*). Species with larger ranges might tend to occupy more habitat types by chance (Gaston 1991; fig. 1, path *d*), especially as range sizes approach biome sizes. Further, as

species’ range limits are more precisely mapped, unsuitable habitat types will be excluded from the distribution maps, reducing overall range size and potentially resulting in an artifactual trend between range size and habitat specificity. A strong correlation between range size and *k* might confound attempts to detect any relationship between *k* and Quaternary climate. We therefore controlled for range size in two ways. First, we included area as an additional predictor variable in the starting model. Second, we removed the effect of area on *k* by calculating deviation from null expectations derived from simulations of range location and size (see app. A in the online edition of the *American Naturalist* for details) and then took contrasts in the residuals. If the deviation of observed *k* from null expectations was significantly correlated with environment, this would suggest a relationship between climate and habitat specificity independent of area (fig. 1, path *b*). However, if range size was determined by habitat specificity (fig. 1, path *c*), controlling for area might obscure any relationship between *k* and climate.

Results

We focus our results on the analysis of contrasts between sister species, excluding threatened and island species (see “Methods”), because we believe that range sizes within this subset of species will best reflect the interaction between climate variables and species’ ecologies. An unavoidable consequence of this constraint is a reduction in sample size from 545 to 296 species pairs. In addition, sister species represent only a fraction of total terrestrial mammal diversity, and results might not extrapolate across all species. However, the geographical distribution of mean sister range sizes correlates closely with that across all mammals ($r = 0.86$ and slope = 1.05 from the correlation of the square root of range sizes for all terrestrial mammals with distribution data, $n = 4,271$, against sister species included in the analyses, $n = 592$, across $0.5^\circ \times 0.5^\circ$ grid cells; see also fig. A2 in the online edition of the *American Naturalist*). In addition, the species analyzed also encapsulate a similar range in environmental variables (fig. A3 in the online edition of the *American Naturalist*).

Averaged across sister species, geographic range sizes were greater at high northern latitudes, a pattern evident in both the Nearctic and the Palearctic (fig. 2), and demonstrated a strong north to south gradient of decreasing size. Notable exceptions to global trends were Northern Hemisphere subtropical desert biomes, for example, the Saharan and Arabian deserts, where range sizes were larger than those at similar latitudes elsewhere. Average range size was generally smaller on islands, even at high latitudes; exceptions include the Hawaiian and Galapagos islands, which support populations of the wide-ranging hoary bat

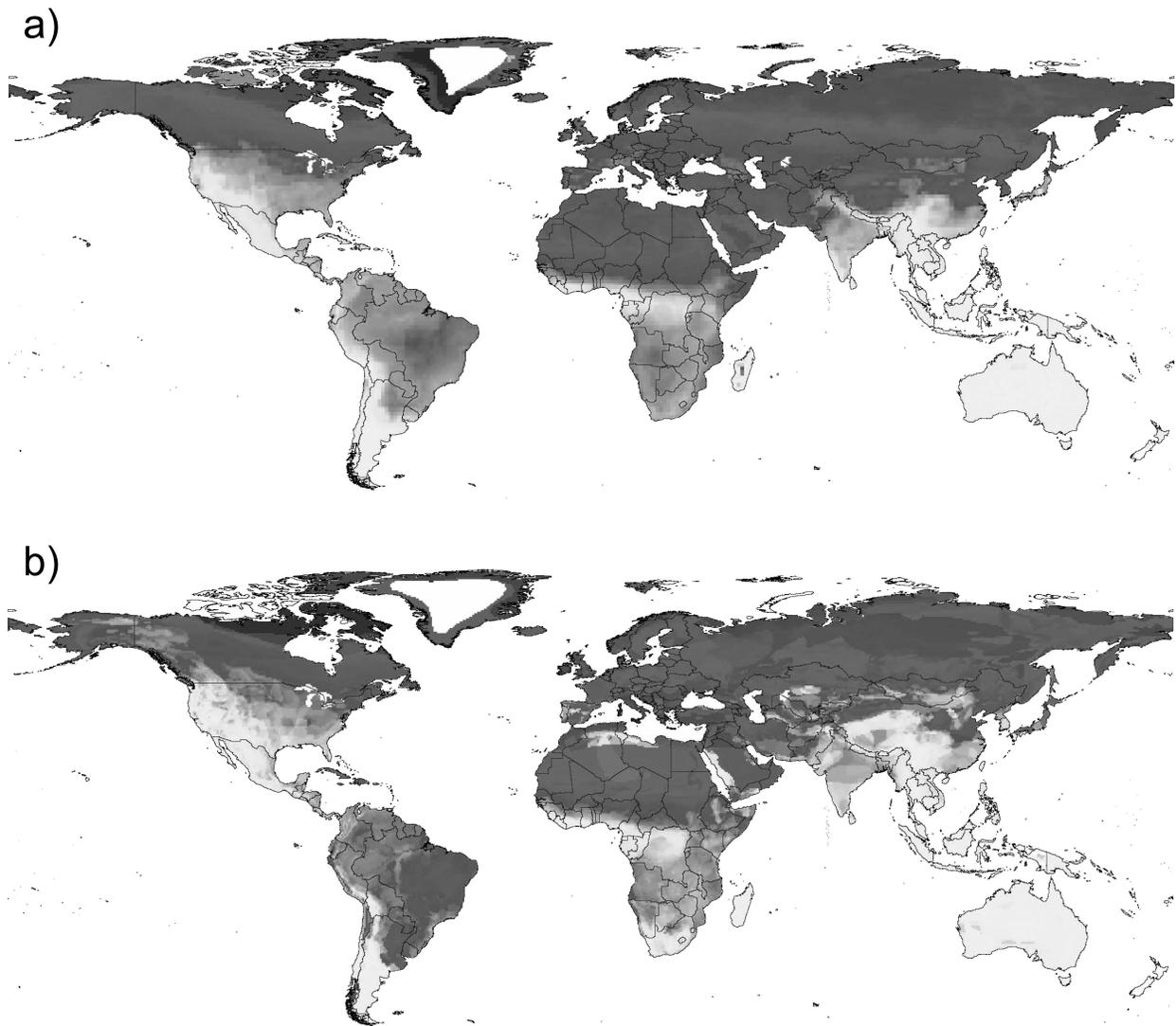


Figure 2: Mean geographic range size (km²) from high (*dark*) to low (*light*) within 0.5° × 0.5° cells for all terrestrial mammals (*a*) and sister species included in the models presented in tables 1–3 (*b*; *n* = 592).

(*Lasiurus cinereus*), the only native terrestrial mammal of Hawaii. Global patterns for sister species matched closely the distribution of range sizes across all terrestrial mammals (cf. fig. 2*a*, 2*b*).

Correlates of Range Size

Species with larger geographical ranges tended to be habitat generalists, but climate was also an important predictor. Contrasts in the environmental variables were intercorrelated ($r = 0.14$ – 0.73 ; fig. A4 in the online edition of the *American Naturalist*), but differences were sufficient to distinguish between them in the models (all VIFs < 5).

Univariate regression models reveal change in temperature since the last glacial maximum (ΔT) to be the best single predictor of range size, with range size increasing with the magnitude of climate change ($r^2 = 0.22$, $p < .01$; table 1). In contrast, range size was negatively correlated with change in precipitation (ΔP ; $r^2 = 0.08$, $p < .01$; table 1). AET and body mass were not significantly correlated with range size. Even when other variables were included in the model, ΔT remained a key predictor of range size, supporting path *a* in figure 1. Globally, range size was best explained by ΔT , habitat specificity (*k*), seasonal variation in temperature (seasonality), and latitude (model 1 in table 2). Species were more likely to have larger ranges in regions

Table 1: Univariate models of contrasts in geographic range size against body mass, habitat specificity (k), and various environmental variables

Explanatory variable	n	r^2	t	p
k	296	.08	5.21	<.001
Seasonality	296	.16	7.57	<.001
ΔT	296	.22	9.04	<.001
ΔP	296	.08	-5.04	<.001
Temperature (T)	296	.06	-4.26	<.001
AET	296	<.01	-1.40	.16
Mass	261	<.01	.69	.49
Latitude	296	<.01	4.40	.06

Note: Excludes contrasts in which one or both sisters were either island endemics or categorized as threatened by the International Union for Conservation of Nature. AET = actual evapotranspiration.

that had experienced large postglacial warming and those that were highly seasonal, both characteristics of high-latitude environments. A negative relationship with latitude indicates a tendency for range size to be greater at lower latitudes after variation in climate and habitat specificity is accounted for. A weak negative correlation with ΔP was lost when we included all sister contrasts (model 1 in table A3 in the online edition of the *American Naturalist*), although the models were otherwise highly congruent (cf. model 1 in table 2 and model 1 in table A3).

Large range size was also positively correlated with greater habitat breadth (model 1 in tables 1, 2), supporting path c or d in figure 1. However, after we adjusted k to correct for expected colinearity with area, assuming no ecological relationship (see app. A), the residual relationship with range size was negative (model 2 in table 2). Larger-ranged species had narrower habitat preferences than expected from their range sizes.

We explored model sensitivity in the following ways. First, because we hypothesized dispersal ability to be a potentially key factor in recolonization and range expansion after glacial retreats (fig. 1), it is possible that range size in bats, which differ greatly from nonvolant mammals in their mode of dispersal, might demonstrate a different relationship with environment. We therefore examined model coefficients including only nonvolant species; while overall explanatory power marginally increased ($r^2 = 0.33$ and 0.37 for the regression including and excluding bats, respectively), the relative strength and direction of the key predictor variables were largely unchanged (cf. model 1 in table 2 and model 1 in table A4 in the online edition of the *American Naturalist*). Second, we controlled for land area, using occupancy as the response variable (see “Methods”). For the global set of sisters, explanatory power was lower ($r^2 = 0.15$), but ΔT remained the key environmental predictor, with k retained as an additional

explanatory variable (model 1 in table A5 in the online edition of the *American Naturalist*). Third, an anonymous reviewer suggested to us that, for species centered in the tropics, larger ranges are more likely to extend toward higher latitudes, potentially resulting in an artifactual trend between range size and high-latitude environments. We therefore repeated our analysis using a single estimate for each environmental parameter from species range midpoints; results were again highly congruent (model 1 in table A6 in the online edition of the *American Naturalist*).

To evaluate the power of our best-fit model to explain range size across all mammals, we compared observed range sizes against expectations from model coefficients derived from the minimum adequate model of contrasts in sister species. We used the model excluding bats as well as threatened and island species (model 1 in table A4), because explanatory power was highest for this model. Our model from contrasts could explain approximately 16% of the variation in range sizes across species (all nonvolant mammals, excluding island and threatened species: $r^2 = 0.16$, slope = 0.20, $F = 432.9$, $p < .01$, $n = 2,346$, from the regression of observed range size vs. predicted range size from the model of contrasts). A scatterplot of predicted versus observed range sizes (fig. A5 in the online edition of the *American Naturalist*) suggests that species fall within two clusters differing in slope, broadly delineating high- versus mid- to low-latitude distributions, in-

Table 2: Minimum adequate models for the regression of contrasts in geographic range size against body mass, habitat specificity (k), and various environmental variables

Model	t	p
1 (response variable = area; $n = 296$; r^2 [adjusted] = .33):		
k	4.43	<.01
Seasonality	4.17	<.01
ΔT	6.30	<.01
Latitude	-3.64	<.01
ΔP	-2.08	.04
2 (response variable = area; $n = 296$; r^2 [adjusted] = .36):		
$k_{\text{residuals}}$	-3.17	<.01
Seasonality	5.64	<.01
ΔT	5.31	<.01
Latitude	-3.13	<.01
3 (response variable = area _{upper third ΔT} ; $n = 94$; r^2 [adjusted] = .36):		
k	5.60	<.01
ΔT	4.26	<.01
4 (response variable = area _{lower third ΔT} ; $n = 30$; r^2 [adjusted] = .36):		
k	3.24	<.01
ΔP	-2.71	.01

Note: Model $p < .01$ in all cases.

dicating that a single global model may be inadequate for predicting range sizes across all mammals (see “Historical Contingency and the Relationship between Range Size and Environment”).

Historical Contingency and the Relationship between Range Size and Environment

Range size among species in regions where Quaternary temperature fluctuations were greatest (falling into the upper third of ΔT) was strongly correlated with ΔT and k in all models (model $r^2 = 0.31$ – 0.41 ; model 3 in table 2 and model 2 in tables A3–A6), supporting path *a* and either path *c* or path *d* in figure 1. In contrast, in regions where Quaternary temperatures were relatively invariant (falling into the lower third of ΔT), species in the most stable environments tended to have the larger range sizes, with ΔP rather than ΔT the better predictor (model 4 in table 2, and model 3 in tables A4, A5). Habitat specificity was also a significant predictor within the latter regions and was the only variable retained within the minimum adequate model using species midpoints (model 3 in table A6). Explanatory power was broadly similar ($r^2 = 0.22$ – 0.48) between models for sisters in the upper third of ΔT and those for sisters in the lower third. In both sets of models, there was mixed support for significant relationships between range size and more contemporary environmental measures, including seasonality, temperature, and AET, when retained in the models; range sizes tended to be larger in cooler, less productive, but highly seasonal environments. Minimum adequate models including threatened and island species were more complex (models 2 and 3 in table A3), and model explanatory power was lower, perhaps reflecting more mixed signals.

Climate Variability and Habitat Specificity (k)

Habitat breadth was strongly correlated with area (model 1 in table 3), supporting path *c* or *d* in figure 1. Species in seasonally variable, colder climates tended to have greater habitat breadth, even after correction for area (table A7 in the online edition of the *American Naturalist*). Postglacial climate change was also a key predictor of k , but it demonstrated a relationship different from that seen with range size. Species in regions that had experienced little postglacial warming but increased precipitation, typical of more equatorial latitudes, tended to have the greater habitat breadth (tables 3, A7). We therefore find no support for the hypothesis that postglacial climate change drives range expansion via its effect on habitat specificity (fig. 1, path *b*–*c*). The relationship between k and environment was broadly similar, even for species in regions with different climatic histories, although there was some

Table 3: Minimum adequate models for the regression of contrasts in habitat specificity (k) against body mass and various environmental variables

Model	<i>t</i>	<i>p</i>
1 (response variable = k ; $n = 296$; r^2 [adjusted] = .23):		
Area	4.57	<.01
Seasonality	2.88	<.01
ΔT	–3.43	<.01
ΔP	2.15	.03
Temperature (T)	–3.13	<.01
2 (response variable = $k_{\text{upper third } \Delta T}$; $n = 94$; r^2 [adjusted] = .34):		
Area	4.16	<.01
Seasonality	3.10	<.01
ΔP	2.57	.02
Actual evapotranspiration	2.45	.02
3 (response variable = $k_{\text{lower third } \Delta T}$; $n = 30$; r^2 [adjusted] = .19):		
Area	2.43	.02
Latitude	2.04	.05

Note: Model $p < .01$ in all cases.

variation in the significant coefficients retained in the minimum adequate models, and explanatory power was greater for species in the lower third of ΔT (models 2 and 3 in tables 3, A7). Seasonality was a highly significant positive predictor of k for species in the upper third of ΔT (model 2 in tables 3, A7), while ΔT and temperature were significant negative predictors for species in the lower third of ΔT (model 3 in table A7).

Discussion

Species’ range sizes vary geographically. Species with the largest ranges are found across high northern latitudes, whereas in Argentina, Madagascar, and Australasia, small-ranged species predominate (see also Davies et al. 2008). A broadly similar global distribution of range sizes has been reported for birds (Orme et al. 2005). The tendency for species’ latitudinal range extents to increase toward the poles has been termed Rapoport’s rule, after Eduardo Rapoport (Stevens 1989). One possible explanation for geographical structure in range size is that species with currently large ranges simply favor biomes that are currently the most geographically extensive (Brown and Lomolino 1998; Gaston 1998). Alternatively, range size might be a product of biological and environmental factors, including dispersal and climatic history.

Climate Variability, Habitat Specificity, and Range Size

Using contrasts between sister species, we show that range size correlates strongly and positively with habitat specificity. The significant relationship between range size and specificity indicates that species' ranges do not simply reflect variation in areas of suitable habitat: either more generalist species can attain larger ranges by occupying a greater breadth of habitat types (fig. 1, path *c*) or species' range sizes are not restricted by the distribution of broad habitat types used in our analysis (fig. 1, path *d*). We also find that range sizes tend to be greater in regions that experienced large Quaternary temperature oscillations but that the correlation between Quaternary oscillations and habitat specificity is negative; species tend to be habitat specialists where Quaternary temperature has been most variable. Therefore, we find no evidence that Quaternary climate oscillations have led to increased geographic range sizes via an effect on habitat specificity (fig. 1, path *b-c*); rather, the influence on mean range size has been direct (fig. 1, path *a*).

By using our measure of occupancy as an alternative response variable, we demonstrate that our results are not an artifact of range size covarying with available area. If more productive environments were capable of sustaining viable populations within smaller geographical regions (Wright 1983), it is possible that this could also result in an association between range size and climate change. However, measures of environmental energy were only marginally significant predictors in the minimum adequate models, suggesting that climate variability is the direct predictor variable. Further, the Sahara, a latitudinal outlier to the global distribution of range sizes, also experienced dramatic climatic shifts, but these were decoupled from higher-latitude climatic oscillations (Kuper and Kröppel 2006).

We conclude that species' ranges have likely been shaped by glacial history and, where Quaternary temperature oscillations have been large, that the magnitude of these oscillations is a dominant predictor of range size. However, the relationship between range size and Quaternary climate cannot be explained by variation in habitat specificity. It is possible that long-term climate change has directly influenced range sizes. For example, Quaternary climate variability may have favored range expansion by altering landscape connectivity (Brown and Lomolino 1998) or by moderating biotic limits to species range extents (e.g., competition and disease), effectively lowering barriers to dispersal. Alternatively, small-ranged species may have been lost disproportionately during glacial cycles because of increased sensitivity to demographic stochasticity (Gaston 2003). Higher rates of extinction at higher latitudes and/or selective recolonization by high-dispersal species

after range contractions would be consistent with the latitudinal gradient in species richness; this trend of decreasing diversity from equator to poles remains one of the most ubiquitous yet least understood patterns in ecology (Hillebrand 2004).

At more equatorial latitudes, the relationship between range size and Quaternary temperature oscillations is lost. Nonetheless, Quaternary climate remains an important predictor, but range sizes tend to be larger where Quaternary climate, as characterized by variation in precipitation, has been most constant. It is possible that non-climatic factors, such as competition, mutualism, and parasitism—long thought important in limiting species' abundances and distributions in tropical biomes (Dobzhansky 1950; MacArthur 1969)—may have restricted recolonization after climatic shifts or prevented species from tracking the changing environment through the Quaternary. Quaternary climate oscillations in the tropics are most evident as changes in precipitation and may have resulted in range contractions but few extinctions. In contrast, at higher northern latitudes, climatic shifts were most evident as changes in temperature and, at the last glacial maximum, a dramatic increase in glacial extent, creating a competition-free landscape that then became open to recolonization as temperatures warmed.

Contrasts between sister species provide a simple but powerful approach to exploring correlations between variables when one or both covary with phylogeny, removing the pseudoreplication that would otherwise result from the phylogenetic nonindependence of the data (Harvey and Pagel 1991). However, spatial autocorrelation might add further nonindependence to the observed data and potentially influence our model parameter estimates. Recently, methods that simultaneously account for both phylogenetic and spatial nonindependence have been proposed (e.g., Diniz Filho et al. 2007; Freckleton and Jetz 2009) and offer an interesting avenue to explore in the future.

Implications for Future Climate Change Scenarios

Our analysis indicates that species' ranges are sensitive to climate change and that large shifts in temperature might ultimately result in species extinctions. If the intensity of future climate change mirrors the geographical distribution of historical change, which may be likely at broad geographic scales relevant to the distribution of species' ranges (Jansson 2003), it might be argued that current estimates of climate-driven extinctions are overly pessimistic. In regions where Quaternary temperature oscillations have been most pronounced, it is possible that many species will have already passed through the climate change "extinction filter" (cf. Balmford 1996) or an equivalent

dispersal filter and that they represent the set of species best suited to shifting ranges in the face of environmental change (Price et al. 1997). Filter effects would provide one explanation for the geographical distribution of “latent extinction risk” across northern North America and the Siberian tundra (see Cardillo et al. 2006), where postglacial climate change has been marked and species appear less threatened than predicted from their biological traits: the more vulnerable species either have already been lost from these regions or have failed to become reestablished.

Unfortunately for present scenarios, one fundamental response to historical climate change has been adaptive shifts in species distributions (Webb and Bartlein 1992; Bennett 1997; Dynesius and Jansson 2000; Davis and Shaw 2001; Jansson and Dynesius 2002). While there is growing evidence of range adjustments in the face of contemporary climate change (Parmesan and Yohe 2003; Root et al. 2003), increasing fragmentation and isolation of natural habitats, in conjunction with the rapid pace of recent warming, will likely prohibit close environmental tracking (Honnay et al. 2002; Jump and Peñuelas 2005). Further, historically less variable regions may be more susceptible to smaller perturbations (Jetz et al. 2007; Williams et al. 2007). Therefore, we suggest that the threat to biodiversity posed by current warming trends may be of greater magnitude than that experienced across Quaternary glacial cycles and that small-ranged species are likely to be most vulnerable.

Conclusions

We show that species in regions that experienced large temperature fluctuations in the Quaternary have large geographic ranges and wide habitat breadths. However, we do not find evidence that Quaternary climate change has influenced species range size via selection on habitat specificity; rather, the relationship between range size and Quaternary climate appears to be direct, and after correction for area, species tend to be more generalist where temperature fluctuated less (fig. 3). Increase in ice cover during glacial maxima and large interglacial oscillations in temperature may have resulted in the loss of small-ranged species through range contraction and extinction, while recolonization favored good dispersers and hence species predisposed to large geographic ranges. In contrast, at more equatorial latitudes, where temperature fluctuations have been less pronounced, species' range sizes tend to be larger where Quaternary climate, as characterized by variation in precipitation, has been most stable (fig. 3). Although Quaternary climate likely influenced species' ranges and community composition at lower latitudes, we suggest that the rapid postglacial range expansion into

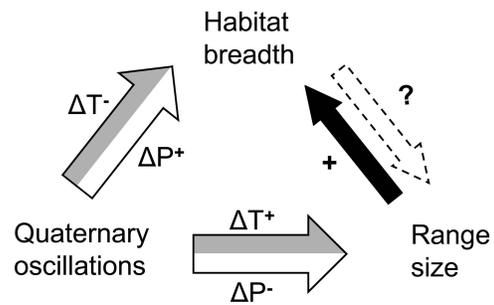


Figure 3: Pathways linking Quaternary climate change, habitat specificity, and geographic range (cf. fig. 1) supported by our regression analysis. Arrows indicate direction of causation; sign of the relationship is indicated by arrow labels. Geographic range size is positively correlated with temperature fluctuations (ΔT) through the Quaternary, but there is no support for an intermediate link with habitat specificity (fig. 1, path *b-c*); instead, the relationship between range size and Quaternary climate appears direct (fig. 1, path *a*).

competition-free space witnessed at higher latitudes was not possible there. The influence of current global warming trends on contemporary range distributions may, in part, be determined by the geographical coincidence between historical and future climate scenarios, but it is likely to be of a magnitude equal to or greater than that experienced across Quaternary glacial-interglacial cycles.

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