

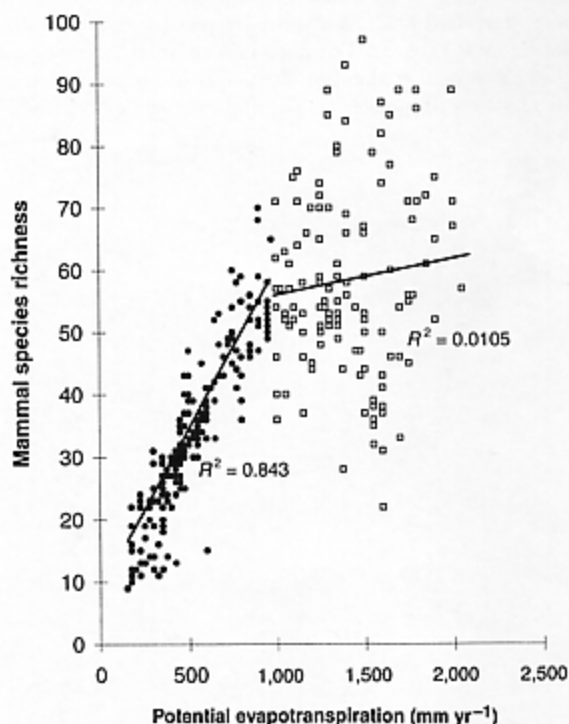
## Habitat heterogeneity as a determinant of mammal species richness in high-energy regions

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A fundamental problem in ecological research is to explain large-scale gradients in species richness<sup>1,2</sup>. Although many causative agents for this phenomenon have been suggested, the species richness–energy hypothesis has received the strongest empirical support<sup>3–6</sup>; this hypothesis states that higher energy availability provides a broader resource base, permitting more species to coexist. Here we show that the species richness–energy hypothesis applies to North American mammals only over a limited geographical area in which climatic energy levels are low (Alaska and most of Canada), rather than on a continental scale as had previously been accepted<sup>6</sup>. In relatively high-energy regions of North America, corresponding to most of the continental United States and southern Canada, we find that mammal species richness is best predicted by topographic heterogeneity and local variation in energy availability. Our results contradict previous studies of large-scale richness patterns that dismissed the importance of habitat heterogeneity<sup>2,7–9</sup>, and have implications for climate change research.

Climatic factors, environmental stability, land area, habitat heterogeneity, historical influences (such as Pleistocene glaciations) and energy availability are the factors most often discussed as determinants of regional variability in species richness<sup>8–13</sup>. Energy



**Figure 1** The relationship between PET and mammal species richness in North America. In areas where  $PET < 1,000 \text{ mm yr}^{-1}$ , PET explains 84% of the variance in mammal richness ( $F = 1.096, P \ll 0.0001$ ). South of this zone, however, PET is unrelated to mammal richness ( $F = 1.35, P = 0.248$ ).

**Table 1** Correlations between environmental factors and mammal species richness in regions in North America

Environmental variable per quadrat <sup>†</sup>	Pearson correlation with MSR‡ in regions where PET $\geq 1,000$ mm yr <sup>-1</sup>	Pearson correlation with MSR‡ in regions where PET < 1,000 mm yr <sup>-1</sup>
Mean annual temperature (1)	-0.392***	0.837***
Mean PET (1)	NS	0.920***
Mean actual evapotranspiration (1)	-0.784***	0.709***
Mean solar radiation (1)	0.353***	0.789***
Mean precipitation (2)	-0.522***	0.318***
Elevation variability (3)	0.808***	0.300***
Precipitation variability (3)	0.344***	0.177*
PET variability (3)	0.615***	0.542***
Annual temperature variability (4)	NS	-0.373***
Glaciation (5)	NS	NS
Longitude	0.698***	-0.150*
Latitude	0.335**	-0.806***
Quadrat area	0.194*	0.238*
Coastal location	-0.176*	-0.571***
Peninsular location	-0.215*	-0.204**

The number after the environmental variable refers to the hypothesis that the variable tests (see Methods). Coastal and peninsular location and quadrat area are control variables; latitude and longitude provide spatial reference. MSR, mammal species richness; PET, potential evapotranspiration, \* $P < 0.05$ ; \*\* $P < 0.005$ ; \*\*\* $P < 0.0001$ ; NS, not significant.

† $n = 130$ .

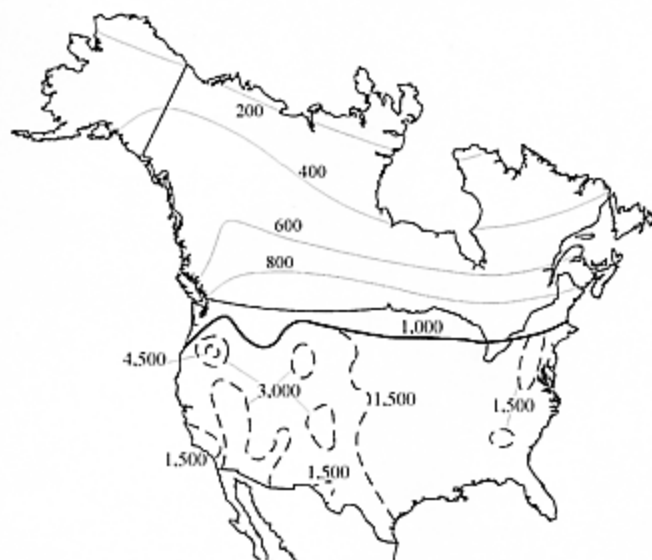
‡ $n = 206$ .

explains most of the observed variance in regional species richness patterns (median  $R^2$  value of 70%, based on 41 studies<sup>14</sup>). Potential evapotranspiration (PET, the amount of water that would evaporate from a saturated surface), an aspect of climatic energy availability, is the best predictor of richness patterns among North American vertebrates, explaining 80% of the geographical variation in mammal species richness<sup>6</sup>. However, inspection of Fig. 1, combined with split-line regression techniques, shows that potential evapotranspiration is closely related to mammal richness when  $PET < 1,000$  mm yr<sup>-1</sup>, but not south of this region (Figs 1 and 2). We therefore investigated other predictors of mammal species richness for higher energy areas south of the PET isocline of 1,000 mm yr<sup>-1</sup>, an area where mammal richness patterns and latitude do not co-vary<sup>15</sup> (Table 1).

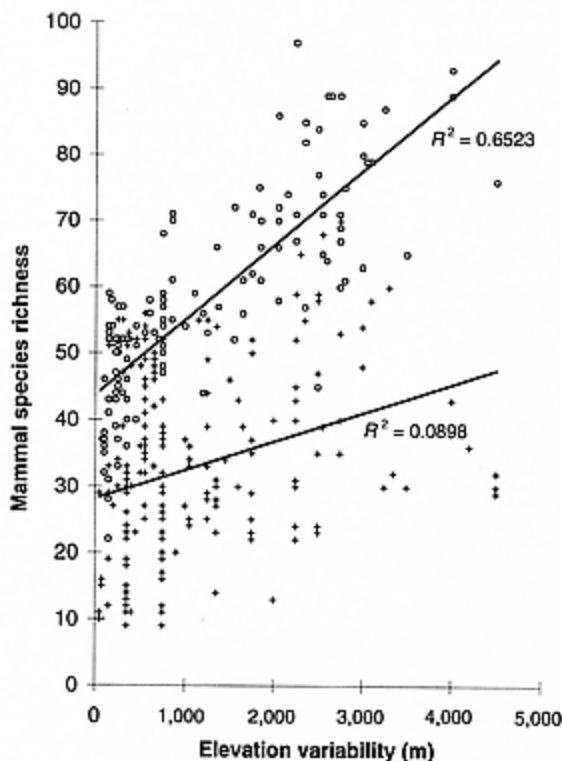
Two aspects of habitat heterogeneity, topographical variation and spatial variability in potential evapotranspiration, emerge from stepwise regression analysis as primary predictors of mammalian species richness (Fig. 3). The high rate at which habitats change along an elevational gradient produces high between-habitat diversity in regions with greater topographic variability<sup>16,17</sup>, leading to

increased regional species richness. Variability in potential evapotranspiration within quadrats may influence mammal species richness through the large-scale co-occurrence of species adapted to different levels of energy availability.

Our results indicate that although there is no single determinant of large-scale variation in mammal species richness, there may be a hierarchical sequence of limiting factors. Our data are consistent with the hypothesis that energy availability limits richness at high latitudes, but that habitat heterogeneity is important when



**Figure 2** A map of North America showing PET patterns (solid curves) in the north (mm yr<sup>-1</sup>) and topographical heterogeneity (dashed curves) in the south (metres). The PET contour at 1,000 mm yr<sup>-1</sup> is in bold. North of this contour, PET is the best predictor of mammal richness, whereas heterogeneity predicts richness to the south.



**Figure 3** The contrasting relationships between mammal species richness and elevation variability, depending on PET levels (crosses when  $PET < 1,000$  mm yr<sup>-1</sup>, and open circles when  $PET \geq 1,000$  mm yr<sup>-1</sup>). In combination with PET variability and coastal location, these factors explain 76.7% of the variability in mammal species richness patterns in high-energy regions of North America ( $F = 138.4$ ,  $P < 0.0001$ ; mammal species richness =  $43.3 + 0.00852 \times$  topographical heterogeneity +  $0.0354$  PET variability -  $9.60$  coastal location). In regions where  $PET < 1,000$  mm yr<sup>-1</sup>, elevation variability is a poor predictor of mammal richness ( $F = 20.12$ ,  $R^2 = 0.0898$ ,  $P < 0.0001$ ).

PET  $\geq 1,000$  mm yr<sup>-1</sup>. Other factors may predict mammal species richness in tropical regions where mammal distributions are relatively poorly known. As potential evapotranspiration in the American southwest is comparable to that of the Amazonian basin<sup>18</sup>, we have sampled almost the entire range of global variation and found that energy is important only in comparatively cold regions.

The nonlinear relationships between diversity and energy availability that we have described may have significant implications for the impacts of climate change on mammal communities. As energy availability increases because of global warming, habitat heterogeneity may become the prime determinant of species richness patterns over an increasing proportion of the North American continent. □

## Methods

**Description of data.** We investigated predictors of mammal species richness in North America using data from ref. 6. We determined the approximate PET contour beyond which PET is unrelated to mammal richness by visual inspection of the PET-richness plot (Fig. 1) and general agreement between the Quasi-Newton, Simplex and Hooke-Jeeves breakpoint estimation routines<sup>19</sup>. The high energy region consists of 130 2.5° × 2.5° quadrats. Independent variables describing mean conditions were determined by averaging maximum and minimum values for the different environmental variables in each quadrat. Those measuring spatial variability were determined by taking the difference between the maximum and minimum values per quadrat for the respective environmental descriptors. Annual temperature variability is the difference between the mean January and July temperatures, respectively, of each quadrat. Glaciation effects were measured by creating a dummy variable describing whether quadrats were clear, inundated or glaciated during the Wisconsinan. Coastal and peninsular location are also dummy variables. Coastal location, in particular, accounts for low richness outliers in our first and third figures.

**Statistical analysis.** We analysed bivariate plots of species richness and the various predictor variables (Table 1) in this region and tested the observed relations using both forward and backward stepwise regression analysis<sup>19,20</sup>. Quadrat area does not enter our final model. Using correspondingly numbered variables in Table 1, we investigated the following hypotheses of species diversity: (1) species richness–energy<sup>21–23</sup>; (2) climatic favourability<sup>5</sup>; (3) habitat heterogeneity<sup>15</sup>; (4) climatic stability<sup>24</sup>; and (5) glacial history<sup>11</sup>. Variation in both elevation and PET are consistently the most important predictors of mammal richness, regardless of the regression approach used. Additional variables may be added to the regression equation, but contribute little to the predictive power of the model.

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