

falling into the increased-variance quadrant. Further, the proportion of clades exhibiting a net increase in species richness is no higher for the increased-variance group than for the directional-change groups (Fig. 3), so the observed patterns are again unlikely to be sampling artefacts. By indicating that patterns are not driven by changes in sample size, these tests suggest that the observed expansions or contractions in size range represent true changes in variance.

The analyses presented here do not support Cope's rule as an evolutionary generalization, and provide the most extensive empirical evidence yet for the 'increased variance' pattern as an equally important pathway in body-size evolution. The selective forces often held to drive Cope's rule (for example, advantages of large size in defence, mating success, predatory ability, and resistance to environmental extremes^{1-4,21,26}) generally imply the evolutionary loss of small-bodied forms. However, the fossil record shows that increases in the maximum body size within clades do not require such mechanisms, but can simply represent one limb of an expanding size range, and that directional decreases in sizes are no less frequent than directional increases. This apparently random evolution of body size in Cretaceous molluscs need not imply the absence of driving mechanisms, but could result from the interaction of many factors which have effects so context specific and scale dependent that unitary patterns fail to emerge¹⁸. Large size is not universally advantageous, and multiple pressures operate on body size and taxon-specific correlates that range from age at first reproduction to allometric morphologies^{13,16}. Thus lineages collectively fail to follow a single, predictable size trajectory as their species diffuse or shift through size changes. Extinction probability also need not be strongly related to size^{24,25}. Despite its importance in microevolution and ecology⁹⁻¹⁴, size plays a surprisingly weak or unpredictable role at larger scales, reinforcing the view that macroevolutionary patterns need not be simple extensions of those seen at the level of individual organisms over microevolutionary time. □

Received 13 May; accepted 23 October 1996.

1. Bonner, J. T. *The Evolution of Complexity* (Princeton Univ. Press, 1988).
2. Benton, M. J. in *Palaebiology: A Synthesis* (eds Briggs, D. E. G. & Crowther, P. R.) 147-152 (Blackwell, Oxford, 1989).
3. Hallam, A. in *Causes of Evolution* (eds Ross, R. M. & Allmon, W. D.) 249-269 (Univ. Chicago Press, 1990).
4. Bush, G. L. in *Evolutionary Patterns and Processes* (eds Lees, D. R. & Edwards, D.) 230-249 (Academic, London, 1993).
5. MacFadden, B. J. *Fossil Horses* (Cambridge Univ. Press, 1992).
6. Norris, R. D. *Paleobiology* 17, 388-399 (1991).
7. Arnold, A. J., Kelly, D. C. & Parker, W. C. *J. Paleontol.* 69, 203-210 (1995).
8. Gingerich, P. D. *Annu. Rev. Earth Planet. Sci.* 8, 407-424 (1980).
9. McLain, D. K. *Oikos* 68, 490-500 (1993).
10. Pimm, S. L. *The Balance of Nature?* (Univ. Chicago Press, 1991).
11. Maurer, B. A., Brown, J. H. & Rusler, R. *Evolution* 46, 939-953 (1992).
12. Brown, J. H. *Macroecology* (Univ. Chicago Press, 1995).
13. LaBarbera, M. in *Patterns and Processes in the History of Life* (eds Raup, D. M. & Jablonski, D.) 69-98 (Springer, Berlin, 1986).
14. Peters, R. H. *The Ecological Implications of Body Size* (Cambridge Univ. Press, 1983).
15. Stanley, S. M. *Evolution* 27, 1-26 (1973).
16. McKinney, M. L. in *Evolutionary Trends* (ed. McNamara, K. J.) 75-118 (Univ. Arizona Press, Tucson, 1990).
17. Gould, S. J. *J. Paleontol.* 62, 319-329 (1988).
18. McShea, D. W. *Evolution* 48, 1747-1763 (1994).
19. Jablonski, D. & Raup, D. M. *Science* 268, 389-391 (1995).
20. Jablonski, D. *Bull. Mar. Sci.* 39, 565-587 (1986).
21. Newell, N. D. *Evolution* 3, 103-124 (1949).
22. Stanley, S. M. *Paleobiology* 12, 89-110 (1986).
23. Vermeij, G. J. & Signor, P. W. *Biol. J. Linn. Soc.* 47, 233-247 (1992).
24. Jablonski, D. in *Evolutionary Paleobiology* (eds Jablonski, D., Erwin, D. H. & Lipps, J. H.) (Univ. Chicago Press, in the press).
25. Gaston, K. J. & Blackburn, T. M. *Phil. Trans. R. Soc. Lond. B* 347, 205-212 (1995).
26. Brown, J. H. & Maurer, B. A. *Nature* 324, 248-250 (1986).
27. Raup, D. M. in *Analytical Paleontology* (eds Gilinsky, N. L. & Signor, P. W.) 207-216 (Paleontological Society, Knoxville, TN, 1991).

Acknowledgements: I thank S. Calzada, R. J. Cleavelly, A. V. Dhondt, D. L. Dockery, C. Heinberg, C. C. Johnson, E. G. Kauffman, G. R. Kennedy, M. Machalski, N. J. Morris, L. R. Saul, N. F. Sohl and G. L. Wingard for access to collections and unpublished information; J. Walsh for assistance with data entry; and W. D. Allmon, M. J. Benton, D. H. Erwin, M. Foote, S. J. Gould, S. M. Kidwell, B. A. Maurer, F. K. McKinney, A. I. Miller, P. Pearson, K. Roy, S. M. Stanley, P. J. Wagner and P. D. Ward for comments. This work was supported by the US National Science Foundation.

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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^{1,2}. Although many causative agents for this phenomenon have been suggested, the species richness-energy hypothesis has received the strongest empirical support³⁻⁶: 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 accepted⁶. 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^{2,7-9}, 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 richness⁸⁻¹³. Energy

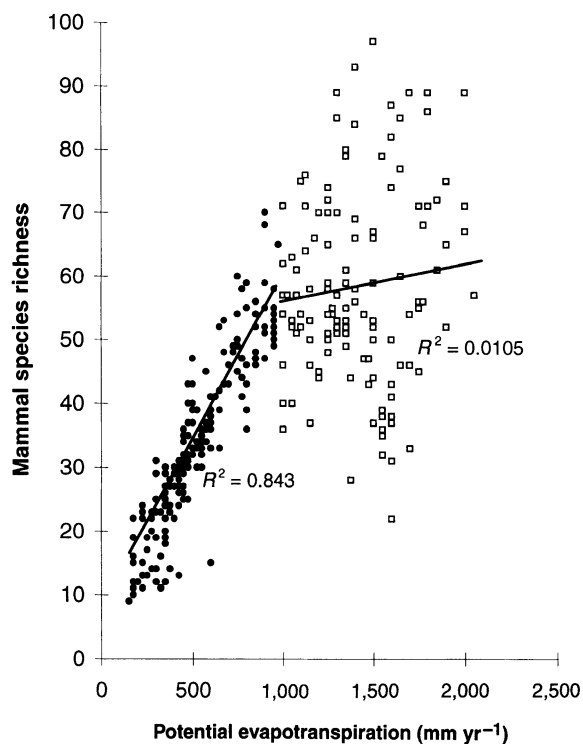


Figure 1 The relationship between PET and mammal species richness in North America. In areas where PET < 1,000 mm yr⁻¹, PET explains 84% of the variance in mammal richness ($F = 1.096, P \ll 0.0001$). South of this zone, however, PET is unrelated to mammal richness ($F = 1.35, P = 0.248$).

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

Environmental variable per quadrat ⁶	Pearson correlation with MSR† in regions where	
	PET ≥ 1,000 mm yr ⁻¹	PET < 1,000 mm yr ⁻¹
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 studies¹⁴). 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 richness⁶. 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⁻¹, 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⁻¹, an area where mammal richness patterns and latitude do not co-vary¹⁵ (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^{16,17}, leading to

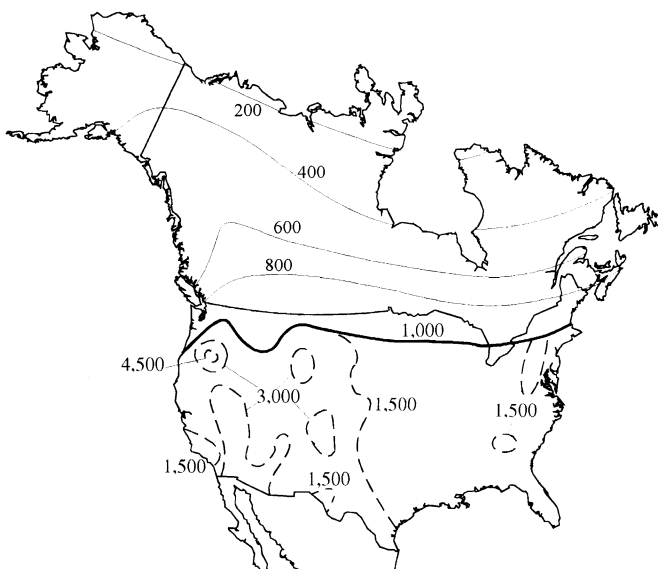


Figure 2 A map of North America showing PET patterns (solid curves) in the north (mm yr⁻¹) and topographical heterogeneity (dashed curves) in the south (metres). The PET contour at 1,000 mm yr⁻¹ is in bold. North of this contour, PET is the best predictor of mammal richness, whereas heterogeneity predicts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

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

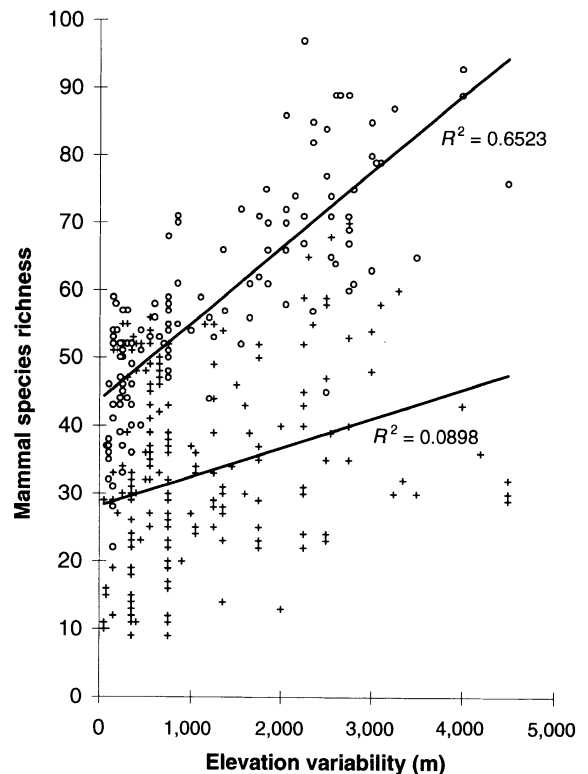


Figure 3 The contrasting relationships between mammal species richness and elevation variability, depending on PET levels (crosses when PET < 1,000 mm yr⁻¹, and open circles when PET ≥ 1,000 mm yr⁻¹). In combination with PET variability and coastal location, these factors explain 76.7% of the variability 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 × topographical heterogeneity + 0.0354 PET variability - 9.60 coastal location). In regions where PET < 1,000 mm yr⁻¹, 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⁻¹. 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 basin¹⁸, 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 routines¹⁹. 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^{19,20}. 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^{21–23}; (2) climatic favourability³; (3) habitat heterogeneity¹⁵; (4) climatic stability²⁴; and (5) glacial history¹¹. 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.

Received 12 August; accepted 27 November 1996.

1. Andrewartha, H. G. *Introduction to the Study of Animal Populations* (University of Chicago Press, Chicago, 1961).
2. Rohde, K. *Oikos* **65**, 514–527 (1992).
3. Currie, D. J. & Paquin, V. *Nature* **329**, 326–327 (1987).
4. Turner, J. R. G., Gatehouse, C. M. & Corey, C. A. *Oikos* **48**, 195–205 (1989).
5. Turner, J. R. G., Lennon, J. J. & Lawrenson, J. A. *Nature* **335**, 539–541 (1989).
6. Currie, D. J. *Am. Nat.* **137**, 27–49 (1991).
7. Stevens, G. C. *Am. Nat.* **133**, 240–256 (1989).
8. Schall, J. J. & Pianka, E. R. *Science* **201**, 679–686 (1978).
9. Adams, J. M. & Woodward, F. I. *Nature* **339**, 699–701 (1989).
10. Wallace, A. R. *Tropical Nature and Other Essays* (Macmillan, New York, 1878).
11. Pianka, E. R. *Am. Nat.* **100**, 33–46 (1966).
12. Huston, M. *Am. Nat.* **113**, 81–101 (1979).
13. Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge University Press, New York, 1995).
14. Wright, D. H., Currie, D. J. & Maurer, B. A. *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schluter, D.) 66–76 (University of Chicago Press, Chicago, 1993).
15. Simpson, G. G. *Syst. Zool.* **13**, 57–73 (1964).
16. World Conservation Monitoring Centre *Global Biodiversity: The Status of Earth's Living Resources* (Chapman & Hall, New York, 1992).
17. Rahbek, C. *Ecography* **18**, 200–205 (1995).
18. *USSR Committee for the International Hydrological Decade Atlas of World Water Balance* (UNESCO, Paris, 1977).
19. StatSoft, Inc. *STATISTICA for Windows* (Statsoft Inc., Tulsa, 1995).
20. Zar, J. H. *Biostatistical Analysis* (Prentice Hall, Toronto, 1984).
21. Hutchinson, G. E. *Am. Nat.* **93**, 145–159 (1959).
22. Connell, J. H. & Orias, E. *Am. Nat.* **98**, 399–414 (1964).
23. Wright, D. H. *Oikos* **41**, 496–506 (1983).
24. Klopfer, P. H. *Am. Nat.* **93**, 337–342 (1959).

Acknowledgements: We are grateful to the Natural Sciences and Engineering Research Council of Canada for scholarship support for J.T.K. and research funding for L.P. We thank D. J. Currie for discussion and for permission to use his climatic and mammal-richness data, M. De Giusti for technical support, and L. Atkinson, B. Fenton and J. Shore for helpful suggestions.

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Impaired auditory recognition of fear and anger following bilateral amygdala lesions

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The amygdalar complex is a medial temporal lobe structure in the brain which is widely considered to be involved in the neural substrates of emotion. Selective bilateral damage to the human amygdala is rare, offering a unique insight into its functions. There is impairment of social perception after amygdala damage, with defective recognition of facial expressions of emotion^{1–4}. Among the basic emotions, the processing of fear and anger has been shown to be disrupted by amygdala damage^{1,2,5}. Although it remains puzzling why this not found in all cases⁶, the importance of the amygdala in negative emotion, and especially fear, has been confirmed by conditioning⁷, memory⁸ and positron emission tomography (PET) experiments^{9,10}. Central to our understanding of these findings is the question of whether the amygdala is involved specifically in the perception of visual signals of emotion emanating from the face, or more widely in the perception of emotion in all sensory modalities¹¹. We report here a further investigation of one of these rare cases, a woman (D.R.) who has impaired perception of the intonation patterns that are essential to the perception of vocal affect, despite normal hearing. As is the case for recognition of facial expressions, it is recognition of fear and anger that is most severely affected in the auditory domain. This shows that the amygdala's role in the recognition of certain emotions is not confined to vision, which is consistent with its being involved in the appraisal of danger and the emotion of fear^{12,13}.

D.R., a woman in her early fifties, first suffered from epilepsy at the age of 28. After anticonvulsant drugs failed to control this, she underwent a series of stereotaxic operations targeted at the left and right amygdala. Tracings of the lesions in the region of the amygdala from magnetic resonance imaging (MRI) scans are shown in Fig. 1.

Following surgery, D.R. could recognize the faces of people who were familiar to her before the operation, and she performed well on unfamiliar face-matching tasks in which the faces had neutral expressions. Hence, there was no general impairment of face perception. In contrast, D.R. showed poor processing of social signals from the face; her judgment of direction of gaze and her interpretation of facial expressions of emotion were impaired^{3,4}. For facial expressions, recognition of fear was differentially severely affected, but there was also evidence of impaired recognition of anger and (to a lesser extent) disgust⁵.

For the present study, we assessed D.R.'s perception of sounds and voices. Audiometric testing was unremarkable, with hearing within normal limits for her age for all frequencies tested (250–8,000 Hz). Tests from the PALPA battery¹⁴ were used to examine D.R.'s auditory processing of language: the results are shown in Table 1. D.R. had no significant problems in discriminating minimally different pairs of