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Testing a mechanistic explanation for the latitudinal gradient in mammalian species richness across North America

A. Marm Kilpatrick,[1,3]* William A. Mitchell,[1,4] Warren P. Porter[1]
and David J. Currie[2]

[1]*Zoology Department, University of Wisconsin-Madison, Madison, WI 53706, USA,*
[2]*Biology Department, University of Ottawa, Ottawa, Ontario K1N 6N5, Canada,*
[3]*Consortium for Conservation Medicine, 460 West 34th Street, 17th Floor, New York, NY 10001, USA*
and [4]*Department of Ecology and Organismal Biology, Indiana State University,*
Terre Haute, IN 47809, USA

ABSTRACT

Hypothesis: Spatial variation in species richness is caused by increased maintenance metabolic costs that increase habitat overlap and decrease species richness.

Organisms: Non-volant mammals in North America.

Results: The latitudinal gradient in species richness could be completely explained by variation in maintenance metabolic costs. Additional spatial variation in species richness was positively correlated with the number of habitats (vegetation types and range in elevation) in an area.

Conclusion: Local processes of habitat selection and habitat availability are important mechanisms determining spatial variation in species richness.

Keywords: energy, evolutionarily stable strategy, mammal, optimal foraging, species diversity, thermoregulation.

INTRODUCTION

Cooler climates are often characterized by a smaller number of species (Currie, 1991; Wright *et al.*, 1993). In part this is a reflection of the well-known latitudinal gradient in species richness (Pianka, 1966; Simpson, 1964; reviewed in Rosenzweig, 1995). But since latitude itself cannot influence richness (Wright *et al.*, 1993; Currie *et al.*, 2004), ecologists have attempted to explain the latitudinal gradient by appealing to factors that vary with latitude. Some of these explanations, such as time since last glaciation or area of biotic provinces (Rosenzweig, 1995; Fraser and Currie, 1996; Rosenzweig and Sandlin, 1997; Ruggiero, 1999; Hawkins and Porter, 2003), do not depend on present-day climates. But many explanations do invoke recent climate or related factors such as temperature, rainfall, solar input, seasonality and productivity (see Hawkins *et al.*, 2003 and references therein). Recent syntheses

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* Author to whom all correspondence should be addressed. e-mail: kilpatrick@conservationmedicine.org

of our understanding of patterns of species richness have shown that indices of temperature and water are often highly correlated with species richness (Hawkins *et al.*, 2003; Currie *et al.*, 2004) for a wide range of taxa, including plants, trees, ectothermic and endothermic vertebrates, and invertebrates. While there are some taxon and geographical differences in the particular variables that show the strongest correlations, heat-related variables (e.g. temperature, potential evapotranspiration) are often highly correlated with the richness of terrestrial vertebrates (Currie, 1991; Hawkins *et al.*, 2003).

These results beg the question, what is the mechanism by which heat could generate and maintain large numbers of vertebrate species? The most frequently cited hypothesis, the energy-richness or more individuals hypothesis (Allen *et al.*, 2002; Currie *et al.*, 2004), is based on an incidence function for species richness that translates heat into species richness by combining two assumptions: (1) the amount of usable heat energy in an ecosystem limits population densities, and (2) the probability that a species persists and can be sampled in an ecosystem is an increasing function of its density (MacArthur and Wilson, 1967; Diamond, 1975; Maurer, 1990; Wright *et al.*, 1993). Increased heat in a region could support increased population densities if individuals became more efficient at transforming food resources into offspring. For example, the density of ectotherm populations could be increased if additional heat energy increased total annual foraging time (Grant and Porter, 1992; Angiletta *et al.*, 2004). For endotherms, heat could increase population densities if it allowed individuals to devote more of their energy to growth and reproduction and less to thermoregulation (Hawkins *et al.*, 2003). However, a recent review of proposed mechanisms underlying climate–richness correlations showed that the energy-richness or more individuals hypothesis was not consistent with patterns of species abundance (Currie *et al.*, 2004), because animal densities were negatively correlated with potential evapotranspiration, whereas species richness was positively correlated with potential evapotranspiration (Currie and Fritz, 1993).

We have previously proposed a different theory linking heat to richness for endotherms (Mitchell, 2000; Mitchell and Porter, 2001). This theory predicts high species richness of endotherms in warmer climates, but not through increased population densities. Instead, higher richness in warmer regions results from lower habitat overlap, which increases the number of species that can co-exist. Our competition model is based on an evolutionarily stable strategy (ESS) model of optimal habitat selection (MacArthur and Pianka, 1966; Rosenzweig, 1981; Brown, 1990). According to this hypothesis, each individual allocates its foraging effort among habitats based on the habitat's profitability, which depends on the densities and foraging behaviour of other individuals. Co-existence of species is possible if individuals of competing species acquire enough energy to cover their maintenance metabolic cost and maintain positive population sizes. In this model, maintenance costs are the rate of energy intake required for an individual to replace itself (on average) in the following generation. The role of heat in this theory is that it determines maintenance metabolic cost through thermoregulation. Maintenance costs determine habitat profitabilities and, as a result, the overlap of habitat use among competitors. Overlap in turn determines whether co-existence of competitors is possible, and thus decreases the richness of the community.

Based on these arguments (for a full presentation of the model, see Mitchell, 2000; Mitchell and Porter, 2001), we predict that low maintenance costs of endotherms in warm climates should allow finer partitioning of spatial heterogeneity by species, leading to increased community invasibility and the co-existence of a greater number of species. Warm climates allow species to divide up the niche axis more finely, while cooler climates result in increased overlap and competition for resources.

The niche overlap model has two advantages over the incidence function model and more individuals hypothesis (Wright *et al.*, 1993; Allen *et al.*, 2002). The first is that it does not require that lower richness of high latitudes coincide with lower average population densities. As noted above, densities increase with latitude and decrease with temperature and potential evapotranspiration, a measure of available ambient energy (Currie and Fritz, 1993). Second, the niche overlap addresses the concern that more benign conditions could result in more individuals, but not necessarily result in a larger number of species (Tilman, 1987; Currie, 1991). We hypothesize that richness is higher in warmer climates due to decreasing maintenance costs and habitat overlap, not as a consequence of increased numbers of individuals. In the niche overlap theory, densities increase as richness decreases and maintenance costs increase (Mitchell and Porter, 2001), which is consistent with the patterns of abundance and richness (Currie and Fritz, 1993; Currie *et al.*, 2004).

Here we test a prediction from this theory, that the species richness of mammals across North America should increase with decreasing maintenance metabolic costs. We test the explanatory strength of this mechanism in two steps. First, we test whether maintenance metabolic rates can account for the latitudinal gradient in species richness. Second, we determine its power to explain the distribution of the number of species of mammals co-occurring within an area after accounting for the effects of productivity and the variation in available habitat (as measured by the number of vegetation classes and the range in elevation; see below for details). In doing so, we are attempting to provide a mechanism for the correlations between species richness and climate indices, which has previously proved difficult (Currie *et al.*, 2004).

MATERIALS AND METHODS

To test the predicted relationship between metabolic maintenance cost and richness, we analysed the distribution of North American non-volant mammals. Because metabolic maintenance costs depend on body size, we divided species into 12 body size categories, and analysed the relationship between maintenance cost and richness for each body size category. We used a heat-transfer model to estimate energetic expenditures for thermoregulation. We then used the modelled metabolic maintenance costs as an independent variable in a series of analyses that also considered the influence of non-metabolic variables on species richness.

Mammal distribution and richness data

Mammal richness data were compiled from range maps (Hall and Kelson, 1959) into a format previously described by Currie (1991). Briefly, the data set includes the presence/absence for species in each of 336 quadrats that are 2.5° longitude by 2.5° latitude south of 50° latitude. North of 50° latitude the latitudinal extent of quadrats was 5.0° to compensate for converging longitudinal meridians and prevent a correlation between quadrat area and latitude. While the resulting quadrats were not all of equal area, multiple regressions showed little effect of quadrat area on species richness (Currie, 1991). Our own regressions using the 12 body size categories also showed little effect of quadrat area on richness after accounting for other explanatory variables (see Results section). In addition, because we analysed the variance and range of some variables, we excluded quadrats that had less than $0.5 \times 1°$ of land inside them because the resolution of our climate and habitat data would only have yielded one data point within the quadrat and prevented a calculation of a range or variance of that variable.

Mammal body size categories

To calculate metabolic maintenance costs, we divided species into 12 body size categories and then calculated metabolic rate for the midpoint of each category. The first ten body size categories represented a doubling of body mass from 0.02 kg up to 10.24 kg. The next two size categories represented a quadrupling of body mass to 40.96 kg and 163.84 kg. Because body size categories were based on even spacing on a log 2 scale, the 0.02 kg category included species with masses ranging from 0.008 to 0.028 kg, the 0.04 kg category comprised species with masses ranging from 0.028 to 0.057 kg, and so on. We chose 12 body size categories in an effort to maintain some accuracy in the estimation of maintenance costs while still including enough species in each category to make the analysis tractable. We assigned each species a mass based on the midpoint of the range for body mass reported in Peterson's *Field Guide for Mammals* (Burt and Grossenheider, 1976).

Climate and geographic data

We obtained climate and geographic data for North America at a resolution of 0.5° latitude and longitude using the following sources: temperature, wind speed, precipitation, cloud cover and relative humidity (Leemans and Cramer, 1991); actual evapotranspiration and potential evapotranspiration [derived using a simple global surface water balance model (Prentice *et al.*, 1993; N. Ramankutty, personal communication) driven using published climate data (Leemans and Cramer, 1991)]; and vegetation type (Haxeltine and Prentice, 1996).

Calculation of metabolic rates

Maintenance metabolic rates were calculated using a previously described model (Porter *et al.*, 1994, 2002). For each grid cell, we input the solar radiation (both direct and diffuse), temperature, wind speed and relative humidity into a microclimate model that generates hourly profiles of the air temperature and wind speed at various heights above ground, as well as soil temperatures from 0 to 60 cm below the surface (Porter *et al.*, 1973). These microclimatic conditions were then used in a model that calculates the metabolic rate of an animal based on several anatomical characteristics. These include body mass, fur depth, fur hair length, hair density, diameter of hairs and fur reflectivity. The fur properties were estimated from allometric regressions given in Kilpatrick and Porter (in prep.). In addition, behavioural parameters were specified, including whether the animal was fossorial, nests, or basks in the sun during daylight hours.

The animal model then calculated the heat generation (metabolic rate) required to maintain the animal's core temperature at 37°C for each hour of the day, for one day each month. This was done by balancing the energy produced by the metabolic rate of the animal with losses to the surroundings through convection, conduction, radiation and evaporation (Porter *et al.*, 1994). If any of the calculated metabolic rates was below the basal metabolic rate (BMR) calculated for an animal with that body mass [$\mathrm{BMR} = 3.41 \times \mathrm{mass}^{0.73}$ (kg) for mammals (Calder, 1984)], then the metabolic rate was set to its BMR for that hour. As a result, the energetic costs of heat stress were not included in the analysis.

To estimate the metabolic maintenance costs or minimum energy requirements, we assumed that mammals in body size categories 1–9 (8 g to 7.07 kg) had access to burrows and nesting materials. Most (72%) of the species in these body size categories were in the well-known fossorial families Rodentia or Insectivora and the others included species that often use burrows [e.g. rabbits, foxes (Hall and Kelson, 1959)]. We calculated the metabolic rate as the minimum of two possible microclimates. The first was the warmest depth in the soil between 0 and 60 cm. Below 60 cm, the temperature of the soil quickly decays to the monthly average temperature (W.P. Porter, unpublished data), making it unnecessary to model deeper soil depths, although many of the larger animals certainly have burrows below 60 cm. The second microclimate was the inside of a nest with a thickness that scaled allometrically with mass$^{0.3}$ at a burrow depth of 20 cm (W.M. Mitchell, unpublished data). We assumed mammals in body size categories 9–12 (>7.07 kg) were able to bask during daylight hours and estimated the metabolic rate assuming that the animal was on the surface and exposed to direct solar radiation. At night, all non-fossorial animals were assumed to rest under the cover of vegetation, thereby avoiding exposure to the radiantly cold night sky. Although these broad assumptions about the burrowing, nesting and basking habitats of mammals do not apply to all species within the respective body size categories, they are representative of the majority of the species in each group.

In summary, we used the energetic model to generate monthly metabolic rates for each of 12 body sizes (20 g to 160 kg), for each $0.5 \times 0.5°$ grid cell in North America, north of Mexico. From this set of 12,268 sites, metabolic rates were combined into 336 quadrats to match the grid of the species distribution data. In doing so, we calculated the average, minimum, range and variance of the metabolic rate for each body size for each quadrat.

Data analyses

To reduce the heteroscedasticity that appeared in plots of richness against predictor variables, we first log-transformed richness. Because some quadrats had zero species for certain body size classes, we were faced with two choices: exclude these quadrats from the analysis, or add a constant before transforming. Adding a constant to small numbers runs the risk of changing the relationship between predictor and dependent variables (Sokal and Rohlf, 1981). In addition, because we were testing a mechanism based on interspecific competition (Mitchell and Porter, 2001), it does not offer insight into differences between sites with zero and one species. As a result, we excluded the quadrats with zero species from the analysis.

We used non-parametric Spearman-rank correlations (which do not assume linearity) of predictor variables and log-richness to determine which months of temperature, actual evapotranspiration and maintenance costs were best correlated with richness (Table 1). Then, in the subsequent multiple regression analysis, we restricted the predictor variables to only these best months, and thereby reduced the multicollinearity of the independent variables. To compare coefficients of different predictors, we standardized all variables by subtracting the mean and dividing by the standard deviation.

In our first analysis, we tested whether maintenance costs could be the mechanism underlying the latitudinal gradient in species richness. We obtained the residuals from a regression of species richness on maintenance costs and calculated the correlation coefficient of the residuals and latitude. If maintenance costs are the mechanism generating the latitudinal gradient in species richness, then our hypothesis predicts that there should be no correlation of the residuals of species richness with latitude. In contrast, if latitude is significantly correlated with residual richness, then additional mechanisms are responsible for the latitudinal gradient. We acknowledge that there is additional spatial variation in mammalian species richness that is not correlated with latitude (Kerr and Packer, 1997).

In our second analysis, we determined the role of an index of productivity [actual evapotranspiration (Rosenzweig, 1968; Currie *et al.*, 2004)] and the number of habitat types available in a quadrat to explain residual variation in mammalian richness. To do so, we used residual or hierarchical regression (Graham, 2003) with four predictors: (1) range of elevations found in the quadrat; (2) number of vegetation types found in the quadrat; (3) linear and (4) quadratic terms for actual evapotranspiration from whichever month was most correlated with richness. We included the quadratic term for actual evapotranspiration because previous studies have suggested that richness often shows a decelerating relationship with productivity [for which actual evapotranspiration is a putative surrogate (but see Hawkins, 2004)], even though the mechanism underlying this curvilinear relationship is unclear (Rosenzweig, 1995).

We examined the spatial autocorrelation in the residuals of our analyses by calculating Moran's I for ten distance classes (Diniz *et al.*, 2003). We set the boundaries of the distance classes so that each class had an approximately equal number of data points. We then compared the magnitude and significance of Moran's I coefficients for the residuals to patterns in the raw data for species richness (Hawkins and Porter, 2003).

RESULTS

Some variables included in our first correlations and early regressions showed little effect and were removed from subsequent analyses. These included area of the quadrat, total area at a latitude (*sensu* Willig and Gannon, 1997) and precipitation (all $P > 0.05$).

The highest correlation of richness with productivity (actual evapotranspiration) generally occurred in April (Table 1). For maintenance costs, July or April was generally best correlated with richness, but January maintenance costs was a better predictor for larger body sizes because there was little geographic variation in these costs during warmer months for large animals (Table 1). The correlation analyses also indicated that, for any given month, richness was better correlated with the maximum values of temperature and actual evapotranspiration, and the minimum value of maintenance costs, than with the average values within quadrats. In other words, what were presumably the most favourable conditions within a quadrat better predicted richness than the average conditions. Therefore, we used the maximum quadrat values of temperature and actual evapotranspiration, and the minimum quadrat value of maintenance costs, as the predictor variables in the analyses.

Not surprisingly, before accounting for any environmental predictors, significant positive spatial autocorrelation in species richness was present at spatial scales of 190–2100 km for BSC 9 and at all scales (190–7500 km) for BSC 6, with other body size categories (BSCs) exhibiting intermediate autocorrelation. Estimates of Moran's I ranged from 0.04 to 0.64 and increased with decreasing spatial scale. Smaller, but significant, autocorrelation remained in the residuals of regressions of richness on maintenance costs at scales of 190–1400 km to 190–2900 km, depending on the body size category. Including additional variables (actual evapotranspiration, elevational range and number of vegetation types) further reduced the spatial autocorrelation so that it was only significant at scales of 190–950 km (the smallest

Table 1. Spearman-rank correlations between mammalian species richness and latitude (Lat), range in elevation within a quadrat (R_{elev}), number of vegetation types (#Veg), actual evapotranspiration (AET), temperature (Temp) and maintenance costs (MC) for each body size category (BSC) with midpoint-mass in kilograms and average number of species/quadrat (#Sp)

BSC	Mass	#Sp	Lat	R_{elev}	#Veg	AET	Month*	Temp	Month*	MC	Month*
1	0.02	8.13	−0.67	0.30	0.42	0.59	April	0.68	July	−0.68	July
2	0.04	4.82	−0.59	0.30	0.38	0.54	April	0.59	July	−0.60	July
3	0.08	2.77	−0.56	0.34	0.46	0.54	April	0.56	July	−0.60	April
4	0.16	3.28	−0.47	0.42	0.52	0.41	April	0.54	July	−0.58	July
5	0.32	1.7	−0.48	0.35	0.43	0.55	January	0.54	April	−0.57	April
6	0.64	1.8	−0.67	N.S.	0.36	0.64	April	0.69	July	−0.68	April
7	1.28	3.75	−0.19	0.35	0.26	0.18	April	0.20	July	−0.37	July
8	2.56	0.86	−0.58	0.40	0.47	0.62	January	0.55	July	−0.59	January
9	5.12	2.79	−0.19	−0.15	0.13	0.49	July	0.21	April	−0.30	April
10	10	5.23	−0.37	0.31	0.51	0.39	April	0.43	April	−0.64	April
11	40	2.56	−0.51	0.49	0.56	0.45	April	0.55	January	−0.59	January
12	160	4.17	N.S.	0.16	0.35	0.22	July	0.12	July	**	

* Refers to the month of the preceding independent variable that had the highest correlation with species richness.
** There was no spatial variability in maintenance costs for this body size.
N.S. = not significant ($P > 0.05$).

distance category) to 190–2550 km depending on the body size category. The significance of the correlation and regression analyses reported below account for the reduced number of degrees of freedom based on the scale of autocorrelation that remained in the residuals.

For 10 of the 11 body size categories below 160 kg (BSC 1–11), richness was more highly correlated with maintenance costs than other predictors (Table 1). In the largest body size category (>160 kg), richness was uncorrelated with latitude and maintenance costs did not vary geographically. As a result, maintenance costs were not considered in other analyses for this body size category (BSC 12). The average magnitude of the correlation coefficients was largest for maintenance costs, slightly less for temperature, and still less for latitude, actual evapotranspiration, number of vegetation types and range of elevation, in that order (Table 1).

For body size categories 1–11, maintenance costs successfully explained the latitudinal variation in species richness; residual species richness was no longer negatively correlated with latitude for any body size category (Table 2). This contrasted sharply to the correlations of species richness with latitude (Table 1). The relationship between maintenance costs and species richness was either linear or quadratic in nature (Fig. 1), suggesting that for some body size categories additional factors may be important in warm areas (Kerr and Packer, 1997).

Including the number of habitats in each quadrat (as measured by the range in elevation and number of vegetation types) and actual evapotranspiration increased the variance explained (R^2) by an average of 12.3% (range 6.4–24%; Table 3). Range in elevation was significant and positive in eight of the body size classes and actual evapotranspiration (either the linear or quadratic term) was significant in 9 of 11 (Table 3). For body size category 12, actual evapotranspiration (AET), the number of vegetation types (#Veg) and the range in elevation (R_{elev}) combined to explain 28.9% of the variation in species richness (Richness = $0.26 + 0.30\text{AET} - 0.26\text{AET}^2 + 0.36\ \#\text{Veg} + 0.15\ R_{elev}$).

Table 2. Regression analysis of species richness on maintenance costs and correlation analyses of the residuals with latitude

BSC	Const.	Linear coefficient	Quadratic coefficient	R^2	Latitude (*r, P*-value)
1	0.23	−0.63	−0.24	75.2	−0.08, 0.16
2	0.17	−0.60	−0.17	63.5	−0.07, 0.22
3	0.00	−0.58	N.S.	33.5	0.04, 0.51*
4	0.00	−0.69	N.S.	47.3	0.05, 0.29*
5	0.16	−0.54	−0.16	39.1	0.04, 0.44*
6	−0.15	−0.83	−0.16	51.8	−0.01, 0.82
7	0.00	−0.51	N.S.	26.1	−0.03, 0.65
8	0.00	−0.59	N.S.	34.9	−0.03, 0.63
9	0.00	−0.34	N.S.	11.5	0.11, 0.05*
10	0.00	−0.70	N.S.	49.2	0.10, 0.07*
11	−0.19	−0.84	0.19	36.1	−0.03, 0.66

* The correlation with latitude was positive, suggesting that a more powerful regressor reversed the sign of the relationship (Sokal and Rohlf, 1981).

N.S. = not significant ($P > 0.05$).

DISCUSSION

The plethora of hypotheses proposed to explain the latitudinal gradient in species richness is nearly overwhelming [over 30 at last count (Hawkins *et al.*, 2003)]. However, a closer look reveals that very few of these hypotheses have been tested, or are even formulated in a manner that is testable (Currie *et al.*, 2004). Here we tested a mechanistic hypothesis that can account for the strong correlations between one aspect of climate (temperature) and spatial patterns of species richness for North American mammals. The analyses were consistent with the hypothesis that broad-scale variation in mammalian species richness in North America may be explained by broad-scale spatial variation in maintenance costs. First, maintenance costs, estimated as the sum of basal and thermoregulatory expenditures of animals in a resting state, were successful in explaining the latitudinal gradient in species richness, leaving no significant latitudinal variation. Second, if this were simply the result of a spurious correlation with richness through another mechanism that acts through temperature, then we would expect that temperature would be more highly correlated with richness. Our analyses suggest the opposite (Table 1). Although our results suggest that increasing metabolic maintenance costs may be the mechanism underlying the strong correlations of mammalian species diversity and climate indices (Currie, 1991), we acknowledge that there may be other important climate-related mechanisms as well, such as increased evolutionary rates at higher temperatures (Rohde, 1992; Allen *et al.*, 2002; Currie *et al.*, 2004).

Our analyses also provide evidence that another simple mechanism, habitat diversity, contributes to the patterns of mammalian richness across North America (see also Kerr and Packer, 1997). The number of habitats within a quadrat as measured by the range in elevation and the number of vegetation types entered significantly into 11 of the 12 body size categories. This mechanism helps to explain the peak in mammalian richness in the west, at similar latitudes to species-poor sites in the eastern United States.

A key issue in analyses of patterns of species diversity is the scale of the analysis (Willis and Whittaker, 2002). We have proposed a mechanism (competition) that acts at local scales in an attempt to explain patterns of regional species richness. Although it is clear that regional

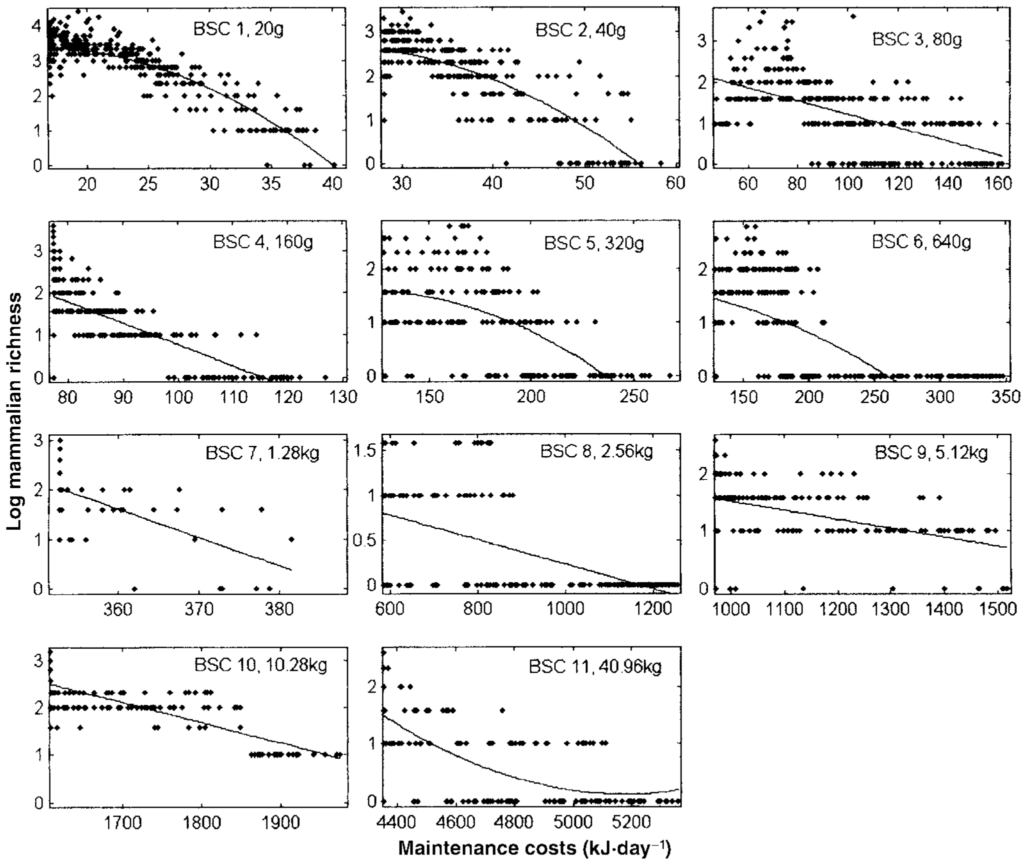

Fig. 1. Log mammalian richness plotted against maintenance costs for 11 body size categories (BSC). Maintenance costs were invariant for body size category 12. See text for details, and Table 2 for coefficients and statistics of fitted relationships.

species richness is influenced by processes such as dispersal, extinction and speciation (Rosenzweig, 1995; Hubbell, 2001; Willis and Whittaker, 2002), our results suggest that local mechanisms may also play a role in broad-scale patterns of species richness. Although the mechanism we propose operates at a local scale, it is driven by maintenance costs, which vary across a broad or regional scale as a function of climate. We believe it is reasonable, therefore, that the effects of this mechanism could be manifest at the regional scale.

Lastly, some researchers have suggested that communities are not saturated with species and so we should not expect local interactions to drive species richness at a regional scale (Rohde, 1992; Lawton, 1999; Willis and Whittaker, 2002). If this is the case, then one is left to formulate a mechanistic model of the factors that are responsible for the spatial variation in the number of species and test it against the hypotheses put forth here. We have been able to show that a mechanism that acts at the local scale, competition, is able to explain the latitudinal gradient in species richness for North American mammals. Several mechanisms are certainly contributing to spatial patterns of richness (Pianka, 1966), but local competition and habitat selection appear to play important roles.

Table 3. Partial regression analysis of species richness after accounting for metabolic costs

BSC	$\mathrm{R}_{\mathrm{elev}}$	AET	AET^2	#Veg	Total R^2
1	1.9^{b}	n.s.	4.5^{a}	n.s.	81.6
2	1.5^{b}	n.s.	5.1^{a}	n.s.	70.1
3	11.0^{a}	n.s.	n.s.	n.s.	44.5
4	11.1^{a}	n.s.	4.4^{b}	1.8^{c}	64.6
5	7.8^{a}	n.s.	2.1^{b}	1.4^{c}	50.4
6	n.s.	4.0^{c}	1.3^{b}	2.7^{a}	59.8
7	3.3^{b}	1.3^{c}	4.8^{a}	n.s.	35.5
8	6.1^{a}	n.s.	n.s.	n.s.	41.0
9	n.s.	12.7^{a}	1.1^{b}	n.s.	25.3
10	n.s.	2.9^{c}	14.9^{a}	6.2^{b}	73.2
11	14.5^{a}	2.9^{d}	1.2^{c}	3.0^{b}	57.7

Note: Values in cells are additional percent variance explained, and total percent variance explained for regressions including only the significant predictors.
^{a,b,c} Superscript letters refer to the order in which a predictor entered the regression.
n.s. = not significant ($P > 0.05$).

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