



Correlates of species richness in North American bat families

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ABSTRACT

Aim A near universal truth in North America is that species richness increases from the Arctic Circle to the Central American tropics. Latitude is regarded as a major explanatory variable in species density, although it is only a surrogate for underlying ecological variables. I aimed to elucidate those underlying ecological variables that are associated with variation in bat species richness across the entire North American continent, providing a portrait of the macroecology of the order Chiroptera and its familial components.

Methods I determined the number of bat species recorded for every state in Mexico and the United States, every province or territory in Canada, and every country in Central America. For each of these entities ($n = 99$), I also gathered basic data on mean annual precipitation, variation across the year (July vs. January) in mean temperature, mean January temperature, range in elevation (topographic relief), per cent vegetative cover and median latitude. Using a variety of linear regression and model-fitting techniques, I analysed the strength and direction of the relationship between species richness and environmental variables for the order Chiroptera as a whole and separately for each of four familial groups: Molossidae (free-tailed bats), Phyllostomidae (New World leaf-nosed bats), Vespertilionidae (evening bats), and a set of six families (the Desmodontidae, Emballonuridae, Furipteridae, Natalidae, Noctilionidae, and Thyropteridae) represented in North America relatively poorly.

Results and main conclusions Save for the Vespertilionidae, species richness of bats increased towards the Panamanian Isthmus. The Phyllostomidae and the set of miscellaneous families are particularly speciose in tropical Central America, with many fewer species occurring through subtropical Mexico into (in some cases) the southernmost United States. The Molossidae extends farther north, sparingly into the middle of the United States. Species density of the Vespertilionidae peaks in central and western Mexico and the southernmost United States, declining south through tropical southern Mexico and Central America and north through the central United States into Canada. Annual precipitation, January temperature, and topography are good predictors of species richness in the Chiroptera and the Molossidae, precipitation, topography, and temperature range in the Phyllostomidae, January temperature and topography in the Vespertilionidae, and precipitation alone in the collection of families. Vegetative cover explained little variation in the Chiroptera as a whole or in any family. After accounting for the effects of the environmental variables, latitude explained an insignificant amount of the residual variation in species richness. Bat families differ in their ecology, so studies of bat biogeography in North America may be misleading if they are examined only at the ordinal level.

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INTRODUCTION

A prominent pattern in species richness in North America is its steep downward gradient from Panama to the pole (Fischer, 1960; Simpson, 1964; McCoy & Conner, 1980; Stevens, 1989; Rosenzweig, 1995). Bats (Mammalia: Chiroptera) are among the mammals that exhibit a striking, near monotonic trend of high diversity (> 100 species) on the Panamanian Isthmus to absence above the Arctic Circle (Fig. 1; Wilson, 1974; Willig & Selcer, 1989; Kaufman & Willig, 1998). Willig & Selcer (1989) examined four predictors of species richness in bats of North and South America. Three predictors – area, latitude, longitude – were geographical, whereas ‘biome richness’ was explicitly biological. They found that only latitude was a good predictor of species richness. In general latitude explained

about three-fourths or better ($r^2 > 0.72$) of the variation in bat species richness, although the relationship was essentially nonexistent for the family Vespertilionidae ($r^2 = 0.03$). Later, Kaufman & Willig (1998, p. 795) concluded that, over the entire order Chiroptera, ‘only latitude is a necessary variable to explain bat richness’.

Yet no taxon responds to latitude *per se*; different taxa instead respond to different environmental conditions found at different latitudes. We must therefore consider climatic factors with a direct bearing on macroecology (*sensu* Brown, 1995), such as mean annual rainfall and seasonal variation in temperature. Altitudinal variation may also have a profound effect on mammalian distribution and richness (Simpson, 1964; Wilson, 1974; Heller & Volleth, 1995; Badgley & Fox, 2000), although again for reasons that different elevations yield

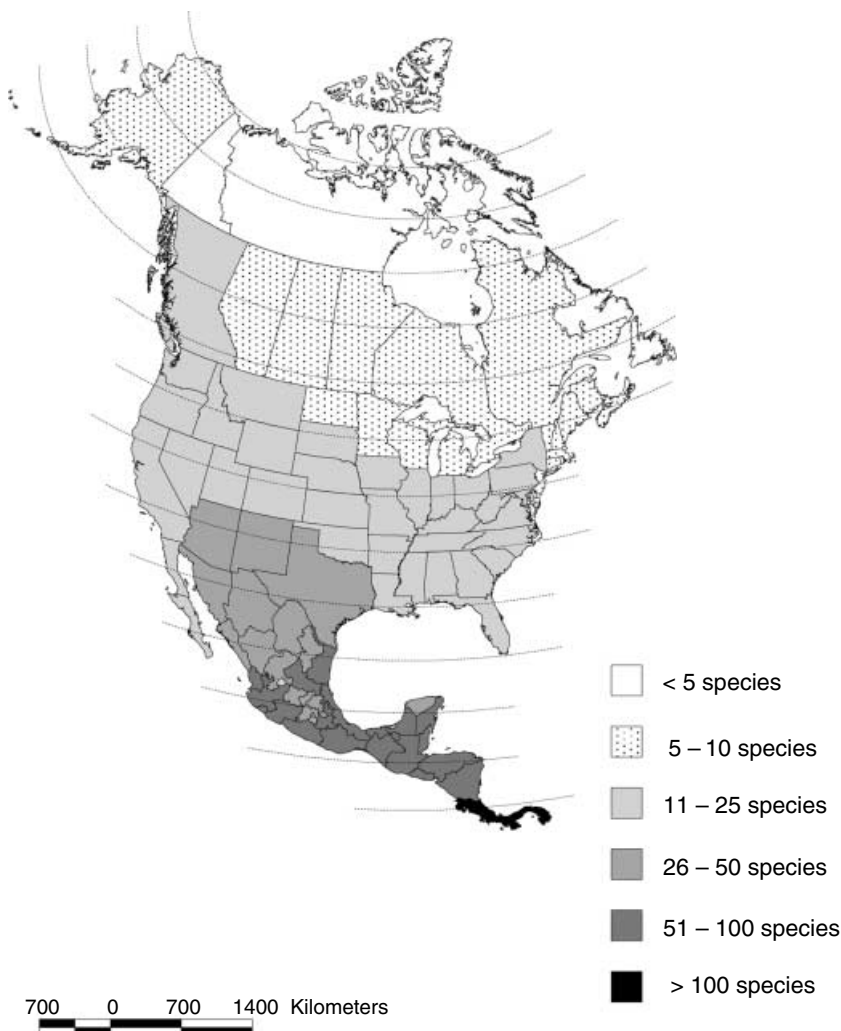


Figure 1 Species richness, in North America, of the order Chiroptera. Dotted lines signify latitude contours spaced at 5° intervals, the southernmost being at 10° N, the northernmost at 70° N. The scale is the same for all maps.

different climatic conditions that affect primary productivity directly. Moreover, the extent of their geographical range is insufficient for comparison among taxa. Largely as a function of extreme differences in productivity, species richness on an expanse of land in Alaska is not comparable with a like-sized expanse in Panama.

Rather than exploring the relationships between bat species richness and geographical features, I was interested in exploring bat macroecology, chiefly the broad-scale environmental factors associated with species richness. Accordingly, on the basis of biogeographical and ecological principles, I developed various predictions for the strength and direction of relationship between bat species richness and climatic variables, elevation and vegetation. I predicted that the association between species richness and

- (1) mean annual precipitation will be strong and positive (justification: high precipitation → high primary productivity → high secondary productivity);
- (2) temperature range will be strong and negative (justification: less seasonal environments are more productive year round);
- (3) mean January temperature will be strong and positive (justification: colder winters → lower food availability);
- (4) range in elevation (the extent of topographic relief) will be weak and positive (justification: larger range in elevation → larger habitat diversity, but most regions have high peaks);
- (5) vegetative cover will be strong and positive (justification: high vegetative cover → high secondary productivity).

The relationship between ecosystem productivity and species richness is complex and nonlinear. Even so, in addition to these thumbnail justifications, Currie (1991) provided a general framework justifying these predictions and outlined theoretical underpinnings of the relationships. Because relationships outlined above are predicated on primary (e.g. plant) and secondary (e.g. arthropod) productivity, they ought to hold particularly well for bat families regardless of the family's ecology (i.e. primarily insectivorous, nectarivorous or frugivorous). Moreover, Badgley & Fox (2000) stressed that environmental variables accounted for much of the apparent latitude gradients in mammal distribution. As a result, I predicted that the five environmental variables I examined would account for enough of variation in bat species richness that latitude would explain a negligible amount of the residual variation.

METHODS

I examined patterns of variation in species richness of bats throughout the North American continent. My base geographical units were provinces and territories in Canada, states in the United States and Mexico, and countries in Central America, a total of 99 geopolitical units. My motivation for using these units was twofold. First, conservation and biodiversity studies tend to stress geopolitical regions. Furthermore, equal-area grids with large cells (e.g. Simpson, 1964) include

much of the ocean adjacent to land masses, yet environmental variables (e.g. surface temperature or annual precipitation) are based solely on the land masses, so these variables do not reflect the whole of the grid. Restricting cells to cover only the land masses renders the grid unequal. Equal-area grids with small cells (e.g. Thompson *et al.*, 1999) include little adjacent ocean but are confounded by a lack of independence between cells, which creates substantial pseudoreplication and, thus, inflation of degrees of freedom in regression or other statistics. Because the geopolitical units in North America differ greatly in size – they generally increase northward – I conducted all analyses on the residual of species richness after the effects of area (\log_{10} transformed) were regressed out (proc reg; SAS Statistical Software ver. 8e; SAS Institute, Cary, NC, USA).

My base taxonomic unit was the family (per Hall, 1981), specifically the Desmodontidae (vampire bats), Emballonuridae (sac-winged bats), Furipteridae (smoky bats), Molossidae (free-tailed bats), Natalidae (funnel-eared bats), Noctilionidae (bulldog bats), Phyllostomidae (New World leaf-nosed bats), Thyropteridae (disc-winged bats), and Vespertilionidae (evening bats). Species richness in the Desmodontidae, Emballonuridae, Furipteridae, Natalidae, Noctilionidae, and Thyropteridae contributed little to the overall pattern in North America, so I lumped their totals into a single unit. I treated the Molossidae, Phyllostomidae, and Vespertilionidae separately. I used Hall's (1981) range maps to obtain the total number of species, by family, occurring in each geographic unit. I used ArcView (ver. 3.3) to create five species density maps for North America, one for the order Chiroptera as a whole, one each for the Molossidae, Phyllostomidae, and Vespertilionidae, and one for the combination of families listed above.

I considered six potential predictors of patterns of bat species richness, each of which varies substantially across North America and thus realistically could be expected to associate with bat species richness. For each geopolitical unit, I obtained estimates of its mean annual precipitation (cm), annual range in temperature (July mean – January mean; °C), range in elevation (highest point – lowest point; m), and an estimate of vegetative cover (%). I also included mean January temperature (°C) as a separate predictor and included median latitude (°). Apart from the vegetation index, which I calculated from the North American Vegetation Index Map (1990, EROS Data Center, United States Geological Survey, and Canada Centre for Remote Sensing), I gathered these basic data from published almanacs and atlases and from online governmental and civic sources, most notably from the EROS Data Center, US Geological Survey (Willmott *et al.*, 1981; Thompson *et al.*, 1999).

I performed separate analyses for the Chiroptera as a whole, and for the Molossidae, Phyllostomidae, Vespertilionidae, and set of additional families. I used multiple regressions to determine the predictive power of each environmental variable, in each case with (residual) bat species richness as the response variable and the environmental variables as

predictors. I used a squared semi-partial correlation (proc reg, SAS) to estimate the contribution of each predictor to the model. I determined the residual effect of latitude in two ways, by comparing the log likelihoods of full models without and without latitude included (proc mixed, SAS) and by regressing out the effects of all environmental variables (proc reg, SAS), then determining how much of the residual was explained by latitude (proc reg, SAS).

RESULTS

Across the order Chiroptera, species richness in North America increases as latitude increases (Fig. 1). Richness is highest in Panama and Costa Rica (both harbour > 100 species); it drops steadily through northern Central America to arctic Canada (Fig. 1). Species richness in the Molossidae (Fig. 2), Phyllostomidae (Fig. 3), and the combination of other families (Fig. 4) show a similar pattern, although in the last two groups richness quickly becomes negligible in the southernmost United States. In contrast to the strong latitudinal gradient that these families exhibit, species richness in the Vespertilionidae peaks around the highlands of

central Mexico and adjacent areas, such as Sonora and Texas (Fig. 5). As a consequence of the latitudinal trend, the relationship between species richness and area was consistently negative and was significant for all but the Vespertilionidae (Table 1).

As predicted, mean annual precipitation is correlated highly positively with bat species richness ($r = 0.57$, $P < 0.001$). Mean precipitation explained an especially high amount of variation in richness in the Phyllostomidae and the combination of families and explained a modest amount in the Molossidae (Table 2). By contrast, there was no association between precipitation and species richness in the Vespertilionidae (Table 2). Associations between bat species richness and mean January temperature range also met predictions, being high and positive ($r = 0.42$, $P < 0.01$) and accounting for nearly half of the variation in richness in the Vespertilionidae (Table 2). The correlation between bat species richness and topographic relief likewise met predictions, being moderate and positive ($r = 0.37$, $P < 0.01$). Range in elevation explained only a modest amount of variation in the Molossidae, Vespertilionidae, and Phyllostomidae but little in the miscellaneous families. Relationships between species

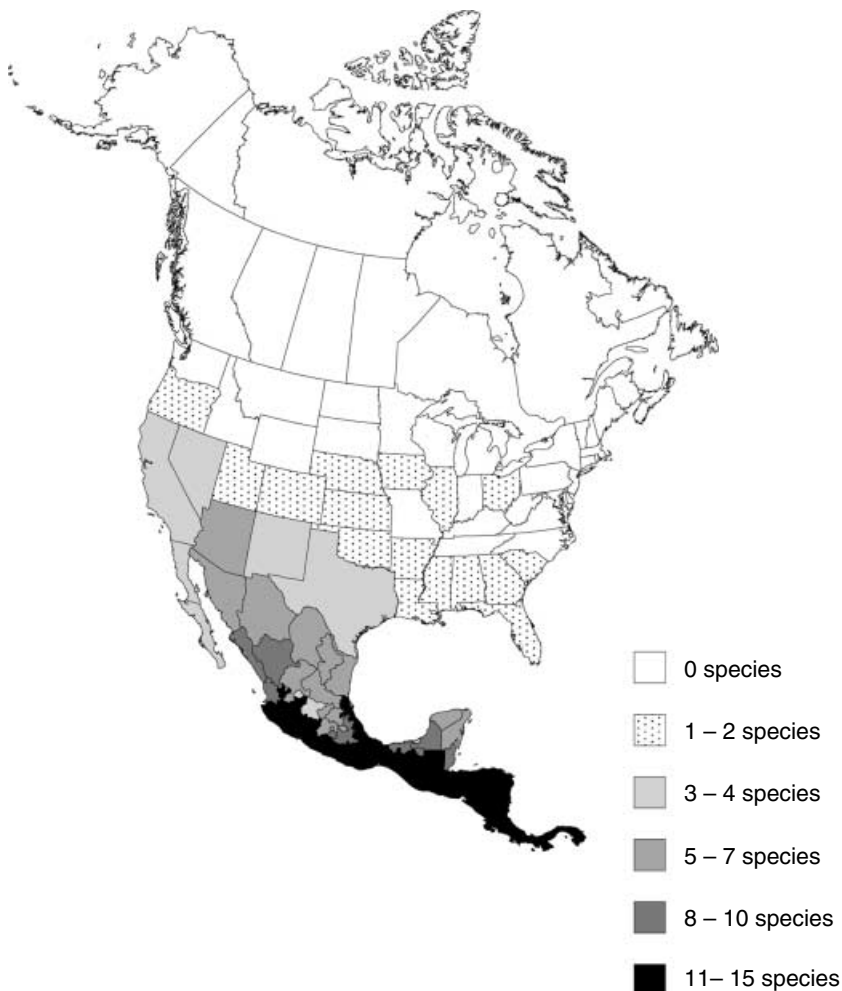


Figure 2 Species richness of the family Molossidae (free-tailed bats).



Figure 3 Species richness of the family Phyllostomidae (New World leaf-nosed bats).

richness and either temperature range or vegetative cover did not meet my predictions. Temperature range was a modest predictor of richness in the Phyllostomidae and Molossidae but was weak for other families (Table 2); vegetative cover explained < 5% of the variation in richness in any family (Table 2).

Latitude had no predictive power once the effects of the environmental variables were included. A model including latitude was no better than a model including only the five environmental variables (Table 3). Moreover, latitude explained an insignificant amount of the residual variation in species richness (Table 4).

DISCUSSION

Species richness and the environment

Results supported predictions for some environmental variables but not others, and support varied among families (Tables 2 and 5). Mean annual rainfall was associated strongly and positively with species richness of North American Chiroptera, specifically the Phyllostomidae and set of families (Desmodontidae, Emballonuridae, Furipteridae, Natalidae,

Noctilionidae, and Thyropteridae). Most of the phyllostomids eat nectar or fruit (Hill & Smith, 1984), so their prevalence in areas with high rainfall – presumably areas of high plant diversity – is logical. With two exceptions (desmodontids eat blood and some noctilionids eat fish, frogs and crustaceans), other bats eat aerial insects (Hill & Smith, 1984). As predicted, richness of North American Chiroptera was associated strongly and positively, specifically the Vespertilionidae and Molossidae. Variation relative to topographic relief also met predictions, being moderately and positively associated with species richness in North American bats. Relationships between richness and either annual temperature range or vegetative cover did not conform to predictions as well as other variables did. In the case of temperature range, relationships were negative but they tended to be weak or moderate, not strong. In the case of vegetation, relationships were weak (moderate for the Vespertilionidae) and tended to be negative, not positive.

As Willig & Selcer (1989) noted, the Phyllostomidae is a typical tropical family – its species richness drops off sharply north of southern Mexico (Fig. 3). Moreover, high richness in this family is associated with high annual rainfall and low fluctuations in seasonal temperatures. The species richness in

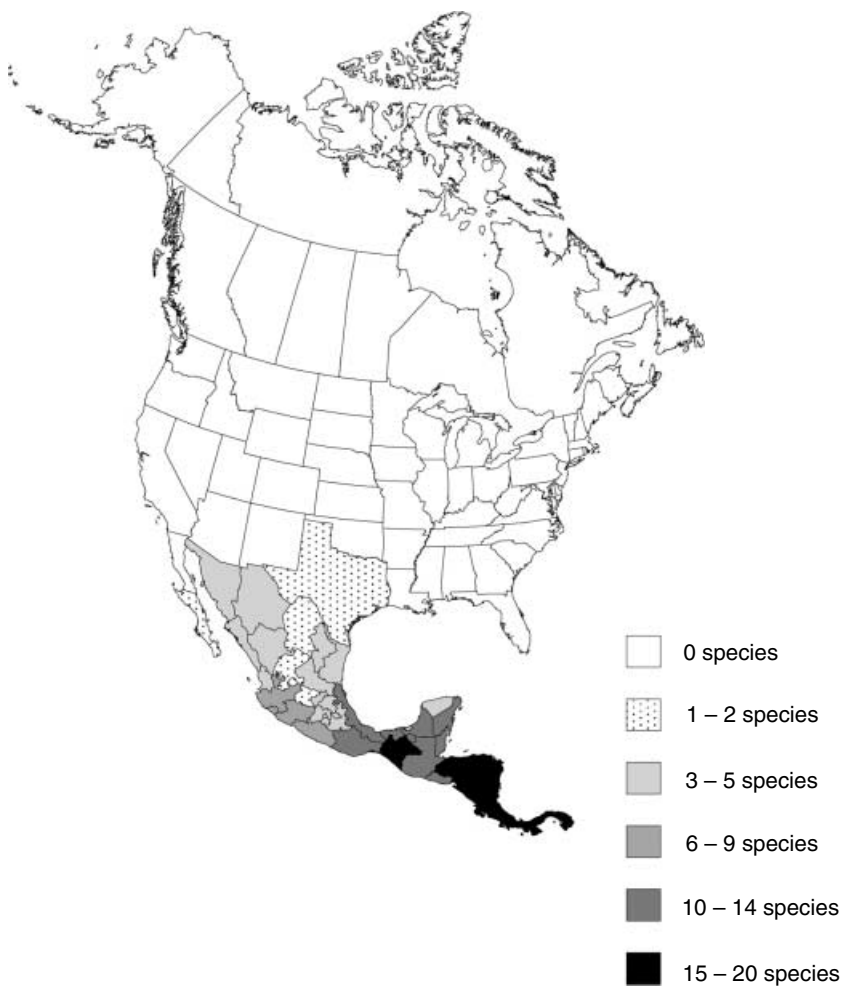


Figure 4 Species richness summed across the families Desmodontidae (vampire bats), Emballonuridae (sac-winged bats), Furipteridae (smoky bats), Natalidae (funnel-eared bats), Noctilionidae (bulldog bats), and Thyropteridae (disk-winged bats).

the set of families varied with annual rainfall as it did in the Phyllostomidae. The Molossidae appears to be more subtropical, with variation in species richness less associated with variation in rainfall and temperature but more associated with variation in winter temperature, suggesting a distribution extending into temperate climes.

In contrast to all of these families, species richness in the Vespertilionidae is associated neither with variation in mean annual precipitation nor with variation in the range of mean winter and summer temperatures. Instead, the family is temperate (Wilson, 1974), meaning it is less associated with variation in rainfall but more associated with variation in temperature. Species in this family rely on insects as a food source, but cold temperatures discourage the development and emergence of insects (Varley *et al.*, 1973). High species richness is associated with regions of higher winter temperature, high topographic relief, and, to some extent, sparser vegetative cover, perhaps accounting for the component species success in central and northern Mexico and the south-western United States (Fig. 5). The family's wide radiation in temperate North America is particularly interesting when considering that, compared with species in more tropical families, the New World vespertilionids are

'restricted in their morphological evolution' (Heller & Volleth, 1995). Although species in this family may not be as morphologically diverse as species in the Phyllostomidae, like many passerine birds they have evolved to take advantage of the high abundance of insects in the north temperate summer.

The latitudinal gradient

I did not include a wide suite of environmental variables; instead, I examined the effects of only five, each of them a crude estimate and each varying substantially across a vast area. Despite this crudeness, I was able to account for enough variation in bat species richness to eliminate the latitudinal gradient (Tables 3 and 4). Latitude still could be used as a surrogate or as shorthand for various environmental factors, but we should not forget that it is merely a surrogate or shorthand. Environmental factors are the actual associates with species richness.

Simpson (1964) asserted that the Vespertilionidae is one of the 'old Holarctic' families that 'reach[es] maximum diversities at various latitudes down to the Tropic of Cancer and become[s] less diverse more to the south' (emphasis in

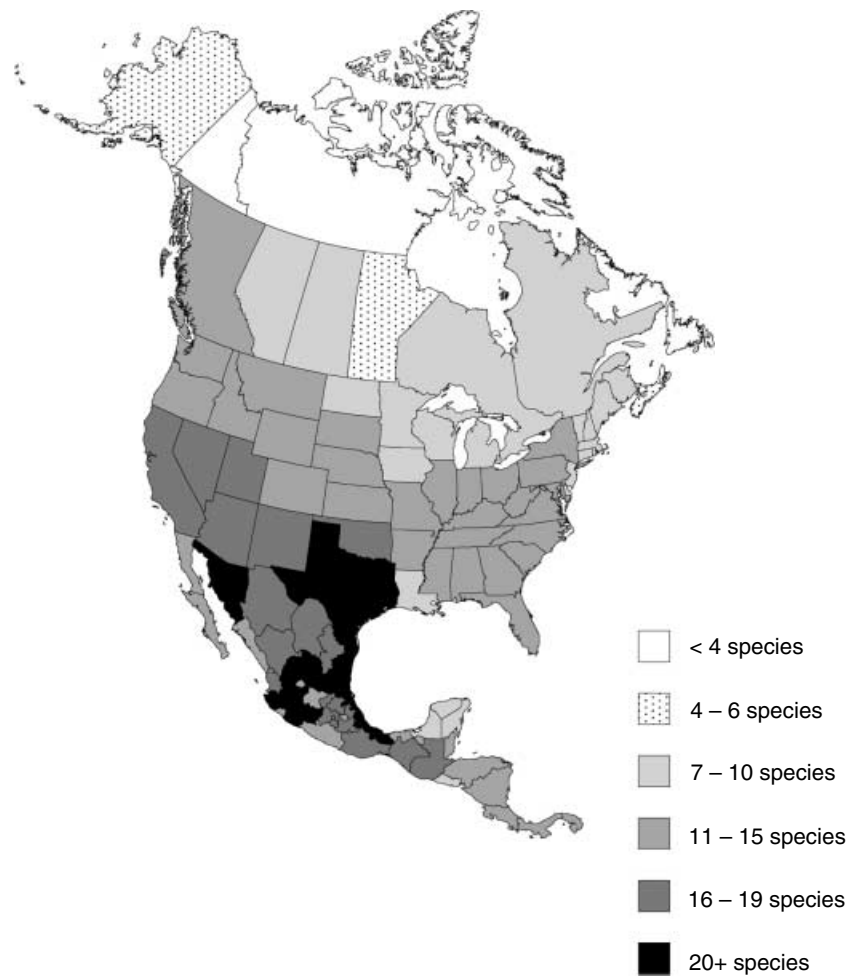


Figure 5 Species richness of the family Vespertilionidae (evening bats).

Table 1 Relationships of $\log_{10}(\text{area})$ of geopolitical units of North America ($n = 99$) and species richness of families of bats. The relationship tends to be weak – for all families area explains under *c.* 10% of the variation in species richness – and is always negative, so the increased area of northern states and provinces does not yield a corresponding increase in species richness

Family	β	SE	R^2	$F_{1,97}$	P
Phyllostomidae	-9.13	2.76	0.102	10.98	< 0.01
Vespertilionidae	-1.18	0.80	0.022	2.16	n.s.
Molossidae	-2.40	0.70	0.106	11.55	0.001
Miscellaneous	-2.23	0.80	0.074	7.71	< 0.01
All bats	-14.93	4.50	0.102	11.00	< 0.01

original). Consequently, analyses of bat species richness to determine the northward limit of Neotropics (e.g. Ortega & Arita, 1998) or to examine latitudinal gradients (e.g. Kaufman & Willig, 1998) may be confounded if data from the Vespertilionidae are pooled with those from other families. In other words, the Vespertilionidae shows a latitudinal pattern quite distinct from other North American families, explaining why plots of species density against latitude are quadratic for that family but linear for other families (Willig &

Selcer, 1989). Were the Vespertilionidae a small family this caution may be unnecessary, but in North America the family trails only the Phyllostomidae in total species richness. The temperate shift in the peak of vespertilionid richness accounts for the secondary peak in overall bat species richness that McCoy & Conner (1980) reported. Still, because the number of North American phyllostomids is well over twice the number of vespertilionids, the former drives the latitudinal trend among North American Chiroptera as a whole. The Chiroptera, in turn, drives much of the latitudinal trend in North American mammals (Wilson, 1974).

The inclusion of all families in analyses of geographical trends may also explain why Wilson (1974) could not find differences in species richness between regions of high and low topographic relief. Richness in the Molossidae, for example, appears to be associated with range in elevation (topographic relief) whereas richness in the miscellaneous families does not. Although Wilson (1974) reported a significant difference in the species richness of bats between regions of high and low actual evapotranspiration, his findings may well have varied had he considered families separately, although at least part of his analyses were confined to the Vespertilionidae (the only bats occurring between 40 and 50° N latitude).

Predictor	Phyllostomidae	Vespertilionidae	Molossidae	Miscellaneous	All bats
Annual rainfall					
β	0.08	0.008	0.004	0.03	0.13
SE	0.03	0.008	0.007	0.01	0.04
R^2	0.376	0.001	0.194	0.446	0.322
Temperature range					
β	-1.30	0.62	-0.23	-0.37	-1.28
SE	0.45	0.12	0.11	0.13	0.69
R^2	0.091	0.039	0.080	0.058	0.056
January temperature					
β	0.13	0.18	0.04	0.09	0.26
SE	0.28	0.08	0.07	0.09	0.43
R^2	0.087	0.457	0.254	0.057	0.178
Elevational range					
β	12.54	3.62	3.61	2.82	22.59
SE	2.50	0.69	0.63	0.75	3.82
R^2	0.109	0.133	0.138	0.074	0.140
Vegetative cover					
β	-0.05	-0.05	-0.02	-0.03	-0.15
SE	0.06	0.02	0.01	0.02	0.09
R^2	0.003	0.044	0.006	0.027	0.010
Median latitude					
β	-0.15	-0.23	-0.10	0.05	-0.42
SE	0.32	0.09	0.08	0.10	0.50
R^2	0.001	0.021	0.006	0.001	0.002
Total R^2 excluding					
Latitude	0.666	0.674	0.672	0.662	0.706

Table 3 Comparisons between models including and excluding latitude as a predictor (\log_{10} of area was regressed out first). All models included annual rainfall, temperature range, topographic relief (\log_{10}), and per cent vegetative cover. For a given bat family, a model excluding latitude is nested within a model including latitude, so statistical significance of adding latitude can be tested as a χ^2 with 1 d.f. (Hilborn & Mangel, 1997)

Family	Model fit ($-2 \log$ likelihood)		χ^2	P
	Latitude included	Latitude excluded		
Phyllostomidae	725.9	725.7	0.2	n.s.
Vespertilionidae	489.9	493.1	3.2	n.s.
Molossidae	472.4	470.8	1.6	n.s.
Miscellaneous	505.0	502.4	2.6	n.s.
All bats	804.0	805.2	1.2	n.s.

That most phyllostomids rely on tropical flowers and fruits for food (Hill & Smith, 1984) may mitigate against that family having a clear relationship with rates of evapotranspiration, which are a function of temperature (Holdridge, 1959) and are strongly correlated with precipitation (Badgley & Fox, 2000). Currie (1991) confirmed this notion: annual potential evapotranspiration explained only about one-third ($r^2 = 0.34$) of the variation in species richness in the Phyllostomidae, yet this variable explained three-fifths ($r^2 = 0.62$) of the variation in richness in the Molossidae and a remarkable nine-tenths ($r^2 = 0.93$) of the variation in

Table 2 Effects of annual rainfall (cm), annual temperature range ($^{\circ}\text{C}$), mean January temperature ($^{\circ}\text{C}$), topographic relief (\log_{10} m), vegetative cover (%), and median latitude ($^{\circ}$) on species richness in bat families (with \log_{10} of area regressed out). β refers to the parameter estimate from a multiple regression; SE is the standard error of that estimate. R^2 values in boldface type signify those parameters explaining >10% of the variation in species richness

Table 4 The explanatory power of latitude after the effects of area (\log_{10}), annual rainfall, annual temperature range, mean January temperature, topographic relief (\log_{10}), and per cent vegetative cover have been removed. Latitude explains < 1% of the residual variance for the Chiroptera or for any of its families

Family	β	SE	R^2	$F_{1,97}$	P
Phyllostomidae	-0.007	0.07	0.0001	0.01	n.s.
Vespertilionidae	-0.011	0.02	0.0031	0.30	n.s.
Molossidae	-0.005	0.02	0.0008	0.08	n.s.
Miscellaneous	0.003	0.02	0.0002	0.01	n.s.
All bats	-0.021	0.11	0.0004	0.04	n.s.

richness in the Vespertilionidae. Currie's (1991) conclusion that 'annual potential evapotranspiration is the best predictor of richness' notwithstanding, his data showed that relationships vary markedly among bat families. I did not include potential evapotranspiration in my models, but it varies with latitude (see Badgley & Fox, 2000) in a manner much like species richness in the Vespertilionidae varies, peaking at roughly 33° N and declining linearly from there towards Panama and the pole.

The numerical dominance of species richness of the Phyllostomidae accounts for the finding that the latitudinal midpoint of the distribution of Chiroptera in North America lies at only 23° N (Pagel *et al.*, 1991). This statement may be accurate exclusive of the Vespertilionidae, but that family's

Table 5 Parameters giving the best models for explaining species richness in families of bats and passerine birds. I assumed that the best model was among the candidate models, so I used the Bayesian information criterion (BIC) to rank all possible models created with the five environmental predictors ($n = 31$ models per family). Probabilities of parameter inclusion were calculated from Schwarz weights derived from model BICs (Burnham & Anderson, 2002)

	Annual rainfall	Temperature range	January temperature	Range in elevation	Vegetative cover
Chiroptera					
Phyllostomidae	x	X	X	X	
Vespertilionidae		X	X	X	X
Molossidae		x	X	X	
Miscellaneous	X			X	
Passeriformes					
Tyrannidae	X		x	X	
Parulidae	X	X	X		X
Emberizidae				X	

X, parameter definitely included ($P \approx 1.0$) in the best model; X, parameter probably included ($0.95 < P < 1.0$); x, parameter possibly included ($0.90 < P < 0.95$).

Table 6 Comparative data for selected speciose families of passerine birds (Aves: Passeriformes). See Fig. 2 for explanations of variables and terms

Predictor	Tyrannidae	Parulidae	Emberizidae
Annual rainfall			
β	0.08	0.06	0.01
SE	0.02	0.01	0.01
R^2	0.326	0.002	0.018
Temperature range			
β	-0.29	1.06	-0.12
SE	0.36	0.23	0.16
R^2	0.037	0.071	0.072
January temperature			
β	-0.22	-0.61	-0.61
SE	0.23	0.14	0.10
R^2	0.086	0.257	0.014
Elevational range			
β	10.60	0.19	7.23
SE	2.04	1.27	0.91
R^2	0.136	0.012	0.315
Vegetative cover			
β	-0.04	0.15	-0.03
SE	0.05	0.03	0.02
R^2	0.005	0.123	0.016
Median latitude			
β	-0.47	-0.54	-0.70
SE	0.26	0.16	0.12
R^2	0.014	0.056	0.158
Total R^2 excluding Latitude			
Latitude	0.590	0.465	0.435

northward shift in distribution (its latitudinal midpoint lies close to 30° N) is lost when all other bat families (whose collective latitudinal midpoint lies close to 20° N) are combined with it into a single taxonomic group (compare Figs 2–4 with Fig. 5). After all, the Vespertilionidae shows a pattern of species density more similar to that of large quadrupeds than that of other bat families (see Wilson, 1974; McCoy & Conner, 1980; Pagel *et al.*, 1991).

Comparisons with Passerine birds

I compared patterns and trends in North American bats with those in North American birds. I also further tested the hypothesis that the five environmental variables could account for a sufficient amount of the gradients in species richness to render inclusion of latitude superfluous. I determined species richness of breeders per geopolitical region (following the American Ornithologists' Union, 1998) for three speciose families of passerines, the Tyrannidae (tyrant flycatchers), Parulidae (wood-warblers), and Emberizidae (sparrows and Old World buntings). I used the same statistical techniques to explore associations between richness and environment.

Unlike bat families, species richness in two passerine families – the Parulidae ($\beta = 2.90$, $SE = 1.16$, $R^2 = 0.06$, $P < 0.05$) and the Emberizidae ($\beta = 1.84$, $SE = 0.91$, $R^2 = 0.04$, $P < 0.05$) – exhibited a strong positive relationship with area of the geopolitical unit, but, as for the Vespertilionidae, richness in the Tyrannidae was not significantly associated with area but the trend was negative. Like bat families, different passerine families exhibited different correlates with the environmental variables (Tables 5 and 6). Richness in the Tyrannidae was similar to that in the Phyllostomidae, being strongly positively associated with annual rainfall and moderately positively with topography. Species richness of the other two families was unlike that of any bat family. Parulid richness was associated chiefly with winter temperature and vegetative cover, whereas emberizid richness was associated with topography and latitude (Table 6).

Unlike the bat families (Table 3) and the other two passerine families, adding latitude to a model including the five environmental variables increased fit for the Emberizidae ($\chi^2 = 28.0$, $P < 0.01$), suggesting that additional environmental variables are needed to explain species richness in the family. Nevertheless, once the effects of the five environmental variables were removed, latitude explained an insignificant amount of the residual variation in species richness of the Tyrannidae ($F_{1,97} = 0.16$, $R^2 = 0.002$), Parulidae ($F_{1,97} = 0.49$, $R^2 = 0.005$), or Emberizidae ($F_{1,97} = 1.32$, $R^2 = 0.013$).

Conclusions

Comparisons between patterns of species richness in bats and passerines underscores two key points. First, environmental variables, even if crude, can explain enough variation in richness to remove all effects of latitude, thus negating the meaning of a latitudinal gradient, except as shorthand for underlying environmental causes. Secondly, patterns across an entire order may be different from patterns in constituent families; indeed, correlates among families may differ from each other to a substantial degree, so much so that very different models explain species richness (see Table 5).

Although Hall's (1981) work likely remains adequate for a broad-brush examination of bat distribution, in light of global climate change (Scheel *et al.*, 1996) and extensive habitat modification (Estrada *et al.*, 1993), the distribution of some species of bats has potentially changed since Hall published his compendium. Even so, I am confident that general patterns I uncovered are real, so my analyses provide not only an important first step towards our understanding of the macroecology of North American bats, but they also underscore the need to be mindful of potential differences in macroecology and biogeography between taxonomic groups, such as families. Indeed, it is possible that more refined analyses would uncover differences in macroecology among, say, subfamilies or genera within the Vespertilionidae or Phyllostomidae.

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