

Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales

Michael R. Willig and Christopher P. Bloch

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The geographic area hypothesis advances area as the primary cause of latitudinal gradients in diversity. The greater area of tropical zones, it suggests, stimulates speciation, inhibits extinction, and leads to increased species richness compared to the situation in smaller temperate and boreal zones. Because bats exhibit exceptionally strong latitudinal gradients of richness at multiple spatial scales in the New World, they are an appropriate system with which to test the geographic area hypothesis. We used range maps for 250 species of New World bats to estimate species richness in biogeographic zones at two hierarchical spatial scales: biome types and provinces. We then conducted a series of regression analyses to evaluate the ability of area to account for latitudinal gradients in species richness. However, spillover (zonal bleeding) of tropical species into extra-tropical zones may mask the species-area relationship and alter perceptions of the latitudinal gradient. To address this issue, we conducted additional analyses excluding tropical species, using a series of increasingly inclusive definitions of tropical ranges. Ecogeographic zones of the New World are not larger at tropical versus extra-tropical latitudes. Moreover, spillover of tropical species into ecogeographic zones within extra-tropical regions generally does not diminish the association between richness and area. Nonetheless, the latitudinal gradient of species richness is strong and significant at both ecogeographic scales. Clearly, area does not drive the latitudinal gradient of bat species richness in the New World. In fact, area represents a source of noise rather than a dominant signal at the focal scale of biome types and provinces in the Western Hemisphere.

M. R. Willig and C. P. Bloch, Dept of Biological Sciences and The Museum, Texas Tech Univ., Lubbock, TX 79409-3131, USA (michael.willig@ttu.edu).

The latitudinal gradient of increasing species richness toward tropical areas may be the oldest and most fundamental pattern regarding life on earth (Rosenzweig 1995, Willig et al. 2003a). It applies to most taxonomic groups; to organisms occupying terrestrial, freshwater, and marine environments; and to biotas in contemporary as well as past time periods (Willig 2000). The exact form of the gradient (e.g. linear, modal, asymptotic) is likely to be scale dependent (Lyons and Willig 2002). Nonetheless, it almost never is one in which richness decreases toward equatorial regions, provided the latitudinal domain is sufficiently extensive (i.e. spans more than 15 degrees of latitude) so as to avoid reflecting local

variation in geography, climate, or edaphic features (Willig et al. 2003a).

In light of the alarming rate at which biodiversity is being threatened as a result of anthropogenic activities, understanding the mechanisms underlying the latitudinal gradient in species richness may be among the most important challenges for biologists in the 21st Century. This is particularly important for bats, as 82% of threatened or microspatial species in the New World are not adequately protected in extant reserves (Andelman and Willig 2003). Moreover, the Chiroptera is the second most species-rich order of mammals, is ecologically diverse, and occupies a variety of functional

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guilds (e.g. frugivores, nectarivores, piscivores, sanguinivores, insectivores, carnivores). In addition, bats provide a number of critical ecosystem services (i.e. seed dissemination, flower pollination, insect control), especially in tropical communities (Patterson et al. 2003, Willig et al. 2003b). Finally, compared to other orders, bats make a disproportionately large contribution to the empirical latitudinal gradient for New World mammals in general (Wilson 1974, McCoy and Connor 1980, Kaufman 1995, Kaufman and Willig 1998).

Considerable contention characterizes the debate about the underlying mechanistic bases that promote the latitudinal gradient of species richness (Rohde 1992, Rosenzweig 1995, Brown and Lomolino 1998, Willig 2000, Schemske 2002). In fact, well over 30 hypotheses – environmental, evolutionary, and stochastic – have been advanced to account for empirical patterns in the latitudinal gradient of diversity (Willig et al. 2003a). Ironically, as certainty about the pattern has increased, the number of competing hypotheses about its cause has increased as well. In part, the increase in the number of hypotheses is understandable; the method of “strong inference” (Platt 1966) cannot be applied easily to the study of such competing hypotheses to reduce the number to a manageable subset of contenders. Because of practical and ethical limitations (Brown 1995), the macroecological study of gradients of diversity is not amenable to the powerful investigative tools of manipulation and experimentation that have catalyzed understanding in other disciplines of biology. Moreover, the primary prediction of most hypotheses related to causes of the latitudinal gradient is that diversity should increase toward the tropics. The form or parameterization of the predicted relationship is not inherent to most hypotheses, with the exception of geometric constraint models (Colwell and Hurtt 1994, Willig and Lyons 1998, Colwell et al. 2004). Thus, secondary or ancillary consequences must be tested to distinguish among hypotheses.

Geographic area hypothesis

One of the most basic ideas that have been offered to account for the latitudinal gradient of species richness is embodied in the geographic area hypothesis. The hypothesis is most associated with Rosenzweig (1992, 1995), although its genesis derives from Terborgh (1973). The fundamental proposition is that tropical zones support more species because they comprise larger areas. The greater area derives from two observations: (1) the circumferences of latitudinal parallels increase toward the tropics, and (2) northern and southern tropical zones are contiguous, whereas those of extra-tropical zones are disjunct. Nonetheless, tectonic movements of continents in conjunction with geological and climatological factors

could (and do) conspire to controvert this pattern. In essence, few question if larger areas are predisposed to support greater richness compared to smaller areas (Brown 1995, Rosenzweig 1995, Brown and Lomolino 1998, Willig 2000); rather a contentious debate has arisen about the extent to which area of ecogeographic zones or other factors drive the latitudinal gradient (Rohde 1997, 1998 vs Rosenzweig and Sandlin 1997).

The mechanistic basis of the geographic area hypothesis is straightforward. Extinction rates should decrease and speciation rates should increase as the size of ecogeographic zones increases (Rosenzweig 1992, 1995, Blackburn and Gaston 1997). Species that occupy large zones can possess large geographic ranges, and thus have higher likelihoods of undergoing allopatric speciation as a consequence of barrier formation. Moreover, such species have higher likelihoods of persisting in niche refugia or enjoying high population densities, thereby reducing extinction probabilities. Zones harboring populations with high rates of speciation and low rates of extinction should support greater species richness. Because tropical species spill over into extra-tropical zones (zonal bleeding), Rosenzweig (1992, 1995) further argued that the species–area relationship should become stronger if tropical taxa are excluded from analyses that are restricted to data for extra-tropical zones. We followed Rosenzweig (1992) in considering the tropical areas to extend between 26° N and 26° S latitude. Consequently, tropical ecogeographic zones are those whose latitudinal mid-points occur within those tropical bounds.

Using bats in the continental New World, we tested three critical assumptions or predictions of the geographic area hypothesis. Specifically, we evaluated (1) if tropical zones are larger than their extra-tropical counterparts, (2) if larger zones harbored greater numbers of species than did smaller zones, and (3) if the correlation between richness and area became stronger when analyses were restricted to extra-tropical zones and non-tropical species (i.e. the spillover effect).

Biogeographic and statistical analyses

Bat distributional data in the continental New World were obtained from a variety of sources, including Hall (1981) for North America and Central America, and Koopman (1982) for South America. These data were modified subsequently as described in Lyons and Willig (1999) by updating range maps using information in Eisenberg (1989) and Redford and Eisenberg (1992). We then intersected the composite range map for each species with a delineation of biogeographic provinces (hereafter provinces) and biome types (hereafter biomes) as defined by Udvardy (1975) for the New World (Fig. 1). This ecogeographic classification is hierarchical,

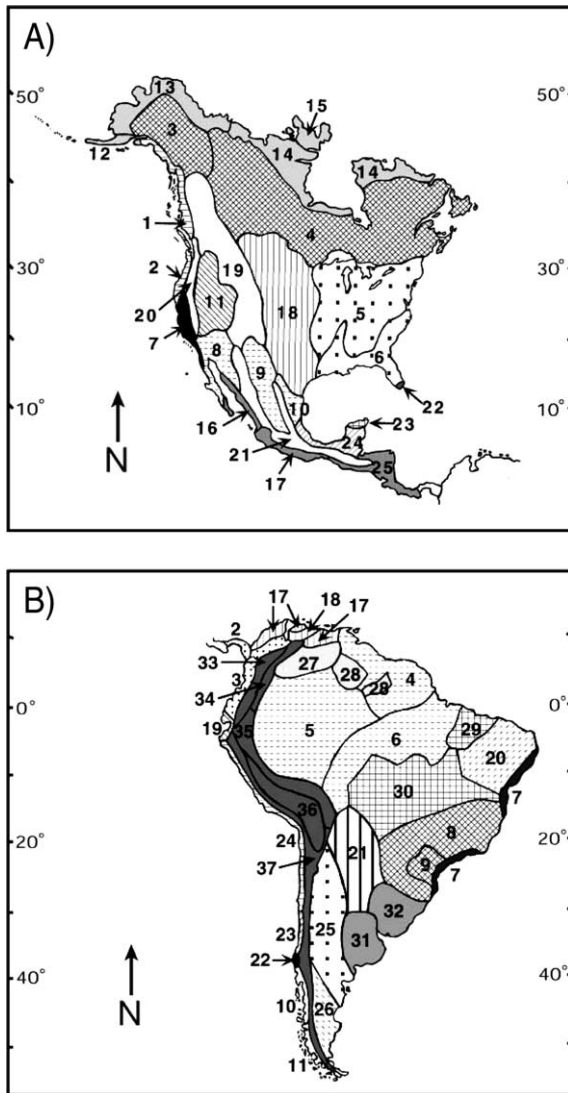


Fig. 1. Map of the New World illustrating the geographic association of provinces with biome types (sensu Udvardy, 1975) in North and Central America (A) as well as in South America (B). Numeric codes for provinces are defined in Table 1. Provinces in the same biome are shaded identically. Distinctive shading represents different biomes.

in that multiple provinces are contained wholly within each biome (Table 1). Moreover, the schema is applied consistently in North, Central and South America, as well as in other continents, making it ideal for broad scale and comparative analyses. To estimate the area of each province, we used a Model 600015 compensating polar planimeter (Keuffel and Esser Co., 1963) with a precision (standard deviation, $n=10$) of 711.3 km² (range of provinces was 8988.9 to 5743874.5 km²). The area of each biome was calculated as the sum of the areas of its constituent provinces. All statistical procedures were conducted in SPSS (1990).

We determined the degree to which area accounted for latitudinal variation in species richness of bats from a variety of regression perspectives. We evaluated if a latitudinal gradient of area exists at the focal scale of biomes or at the focal scale of provinces by regressing area on the mid-point in the latitudinal extent of an ecogeographic zone (mid-latitude). Regardless of the outcome of those analyses, we evaluated if variation in area accounted for a significant amount of variation in species richness of biomes or of provinces using regression analysis. Both species richness and area were log-transformed in these analyses because of the assumed power relationship (Arrhenius 1921, 1923a, 1923b) between them in many biogeographic and ecological studies (Gilbert 1980, Rosenzweig 1995). We executed regression analyses at each of the two focal scales from a number of taxonomic perspectives including all bats, as well as bats in each of the three most species-rich families in the New World, the Molossidae, Phyllostomidae, and Vespertilionidae (Koopman 1993). Because other mathematical models may be more appropriate representations of an empirical species–area relationship (Coleman et al. 1982, Scheiner 2003), we also executed assessments of the effects of area on species richness based on the exponential or semi-logarithmic relationship (Gleason 1922, 1925). As statistical conclusions concerning species–area relationships did not differ between assessments based on power or semi-logarithmic models, we present results regarding only analyses based on the former.

We evaluated the spillover effect (Rosenzweig 1992, 1995) separately for all bats, as well as for molossids, phyllostomids and vespertilionids. We did so by excluding tropical species from estimates of species richness and by focusing on extra-tropical zones. The attribution of “tropical” to species based on considerations of ecogeographic distribution is somewhat arbitrary, but can have a critical impact on analytical conclusions (Blackburn and Gaston 1997, Ruggiero 1999). As a consequence, we considered a broad range of restrictive definitions before considering a species to be tropical. More specifically, tropical designations were recognized at four levels: 1) those species whose distributions are wholly tropical, 2) those species for which at least 75% of their spatial distribution is tropical, 3) those species for which at least 50% of their spatial distribution is tropical, and 4) those species for which any portion of their spatial distribution is tropical. For each combination of taxon and tropical designation, we conducted a log-log regression analysis between species richness and area for extra-tropical zones and compared results to those from identical analyses based on all species regardless of their tropical affiliation. Only zones in which species richness exceeded zero were included in analyses for a particular combination of taxon and

Table 1. Hierarchical association of provinces with biomes based on the classification scheme of Udvardy (1975). Provinces conform to Udvardy's "biogeographic provinces" and biomes to "biome types," except where a single biome type comprises multiple geographically disjunct subsets. In such cases, we consider each as a distinct biome unless the disjunction is small. Mid-latitude is the latitudinal midpoint of a province; latitudes in the northern hemisphere are positive, whereas those in the southern hemisphere are negative. S indicates species richness of a province. Map ID refers to the number that identifies each province on Fig. 1. NA and SA identify on which map (North America (Fig. 1A) and South America (Fig. 1B), respectively) the province appears.

Biome	Province	Area (km ²)	Mid-latitude	S	Map ID
North American temperate rain forests	Sitkan	287 643.17	50.0	16	
	Oregonian	143 821.58	55.5	8	NA1
Temperate needle-leaved forests			43.0	16	NA2
			56.0	10	
	Yukon taiga	1 240 461.16	64.5	2	NA3
North American temperate broadleaf forests	Canadian taiga	5 743 874.50	54.5	10	NA4
			36.5	17	
North American evergreen sclerophyllous forest/scrub	Eastern forest	2 432 981.79	39.5	17	NA5
	Austroriparian	808 996.41	31.0	17	NA6
North American warm deserts/semi-deserts	Californian	224 721.23	35.5	24	NA7
			29.0	74	
North American cold-winter deserts/semi-deserts	Sonoran	539 330.94	31.0	40	NA8
	Chihuahuan	674 163.67	28.5	50	NA9
	Tamaulipan	203 747.24	25.5	61	NA10
Tundra	Great Basin	844 951.81	41.5	19	NA11
			41.5	19	
North American tropical dry/deciduous forests 1	Aleutian Islands	62 921.94	64.0	2	
	Alaskan tundra	820 981.54	57.0	1	NA12
	Canadian tundra	1 276 416.56	65.0	1	NA13
	Arctic archipelago	206 743.53	63.5	2	NA14
			69.0	1	NA15
North American tropical dry or deciduous forests 2			18.5	117	
	Sinaloan	143 821.58	25.0	54	NA16
	Guerreran	233 710.07	18.5	82	NA17
	Central American	398 505.64	11.5	117	NA25
North American tropical dry or deciduous forests 3	Everglades	8988.85	25.5	7	
			25.5	7	NA22
North American temperate grasslands	Yucatecan	35 955.40	21.0	40	NA23
			21.0	40	
North American mountain systems	Grasslands	2 777 554.34	39.5	27	NA18
			39.5	27	
	Rocky Mountains	1 854 699.17	36.5	123	
	Sierra-Cascade	206 743.53	46.5	22	NA19
North American tropical humid forests	Madrean-Cordilleran	782 029.86	42.5	18	NA20
			24.5	119	NA21
			19.5	92	
South American tropical humid forests 1	Campechean	326 594.85	19.5	92	NA24
			4.0	133	
South American tropical humid forests 2	Panamanian	62 191.14	8.5	101	SA2
	Colombian coastal	232 540.79	4.0	128	SA3
South American tropical humid forests 3			-2.0	155	
	Guyan	970 722.61	5.5	127	SA4
	Amazonian	2 733 706.29	-4.0	133	SA5
	Madeiran	1 833 286.71	-8.5	121	SA6
South American temperate rain forests 1	Serra do mar	189 277.39	-25.5	77	SA7
			-25.5	77	
South American temperate rain forests 2	Brazilian rain forest	1 749 463.87	-23.0	83	SA8
	Brazilian planalto	243 356.64	-23.0	82	SA9
			-25.0	59	
South American tropical dry/deciduous forests 1	Valdivian forest	73 006.99	-47.0	6	SA10
	Chilean Nothofagus	100 046.62	-42.5	6	SA11
South American tropical dry/deciduous forests 2			-51.5	4	
	Venezuelan dry forest	300 139.86	10.0	124	SA17
	Venezuelan deciduous forest	73 006.99	10.0	122	SA18
South American tropical dry/deciduous forests 3			10.0	117	SA18
			-3.5	69	
South American tropical dry/deciduous forests 4	Equadorian dry forest	59 487.18	-3.5	69	SA19
			-3.5	69	
South American temperate broadleaf forests	Caatinga	1 030 209.79	-9.0	80	SA20
			-9.0	80	
South American evergreen sclerophyllous forest/scrub	Gran chaco	1 081 585.08	-24.5	65	SA21
			-24.5	65	
South American warm deserts/semi-deserts 1	Chilean <i>Araucaria</i> forest	27 039.63	-37.0	6	SA22
	Chilean sclerophyll	48 671.33	-37.0	6	SA22
			-33.0	7	
			-33.0	7	SA23
			-18.0	35	
	Pacific desert	210 909.09	-18.0	35	SA24

Table 1 (Continued)

Biome	Province	Area (km ²)	Mid-latitude	S	Map ID
South American warm deserts/semi-deserts 2			-33.5	27	
	Monte	1 260 046.62	-33.5	27	SA25
South American cold-winter deserts/semi-deserts			-46.5	5	
	Patagonian	459 673.66	-46.5	5	SA26
Tropical grasslands 1			5.0	121	
	Llanos	438 041.96	6.0	117	SA27
	Campos limpos	356 923.08	4.5	113	SA28
Tropical grasslands 2			-11.5	100	
	Babacu	319 067.60	-4.0	74	SA29
	Campos cerrados	2 036 083.92	-14.5	95	SA30
South American temperate grasslands			34.0	28	
	Argentinian pampas	567 832.17	-36.0	14	SA31
	Uruguayan pampas	543 496.50	-31.0	28	SA32
South American mountain systems			-21.5	163	
	Northern Andean	275 804.20	2.5	138	SA33
	Colombian montane	154 125.87	3.5	139	SA34
	Yungas	559 720.28	-10.0	123	SA35
	Puna	570 536.13	-15.0	108	SA36
	Southern Andean	740 885.78	-27.5	68	SA37

ecological scale. Consequently, sample sizes differed among analyses.

Even though the pattern is well-documented at a number of geographic scales in the New World (Wilson 1974, McCoy and Connor 1980, Willig and Selcer 1989, Willig and Sandlin 1991, Kaufman and Willig 1998, Lyons and Willig 1999, 2002), we evaluated the latitudinal gradient in species richness at two ecological scales for all bats, as well as for phyllostomids, molossids, and vespertilionids separately, using linear regression analyses. We did this at the focal scales of biomes and of provinces, with the entire continental Western Hemisphere as the extent of the analyses. Nonetheless, analyses included only zones in which species richness exceeded zero for a particular combination of taxon and ecological scale.

Latitudinal trends of area for ecogeographic zones

Biomes and provinces exhibit considerable variation in area and species richness (Table 1). Biomes range in size by almost three orders of magnitude, from 8989 km² (North American tropical dry or deciduous forest biome) to 6 984 336 km² (temperate needle-leaved forest biome), whereas provinces range in size by almost three orders of magnitude, from 8989 km² (Everglades Province) to 5 743 875 km² (Canadian taiga Province). Similarly, the richnesses of bat faunas that occupy biomes span almost two orders of magnitude, from two species (tundra biome) to 163 species (South American mountain biome). Those occupying provinces span over two orders of magnitude, ranging from one species (Aleutian Island, Alaskan tundra and Arctic archipelago provinces) to 139 species (Colombian Montane Province).

Neither biome area nor province area were correlated significantly with mid-latitude (Fig. 2A, 2B), suggesting that area has little to do with the well-documented latitudinal gradient of species richness in New World bats, or of any other of the numerous taxa that exhibit strong latitudinal gradients in the Western Hemisphere (reviewed by Willig et al. 2003a). Nonetheless, for analyses conducted at two ecogeographic scales, latitude's signal was clear – mid-latitude accounted for significant and appreciable variation in species richness at the level of biomes and that of provinces for all bats (Fig. 2C, 2D), as well as for each of the three most species-rich families.

Variation in log of species richness as a consequence of variation in log area was not significant for all bats at the ecogeographic scale of biomes ($B_1 = 0.22$, $r^2 = 0.08$, $P = 0.116$; Fig. 2E) or provinces ($B_1 = 0.16$, $r^2 = 0.02$, $P = 0.290$; Fig. 2F). At the familial level, the variation in log species richness related to variation in log area was similarly low, ranging from <0.01 for phyllostomids at the scale of provinces to 0.19 for molossids at the scale of biomes. Familial analyses were not significant, except for those of molossids and vespertilionids at the scale of biomes, and even in these cases, the proportion of variation in log species richness related to log area was not particularly large, equalling 0.19 and 0.14, respectively.

Finally, evidence in the New World does not support the prediction of a spillover effect for bats. The strength of the relationship between species richness and area of extra-tropical zones is little affected by the exclusion of tropical species from analyses, regardless of the criterion used to define "tropical" (Table 2) for both biomes (Fig. 3) or provinces (Fig. 4). For all bats at the focal scale of biomes, the log-log relationship between richness and area is significant ($r^2 = 0.40$; $P = 0.03$) when all species with any portion of their range in tropical biomes

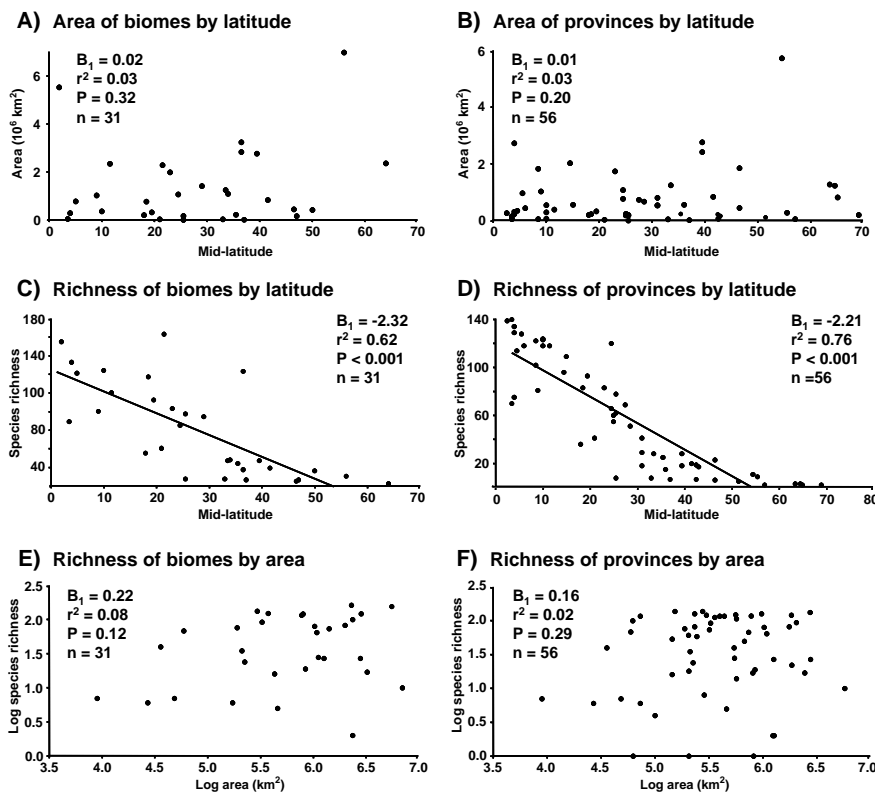


Fig. 2. Scatterplots of area by mid-latitude (A and B), species richness by mid-latitude (C and D), and log species richness by log area (E and F) for New World bat species richness of biomes (left column) and provinces (right column). Regression lines indicate significant relationships at an alpha of 0.05. No distinction was made between northern and southern mid-latitudes in these analyses.

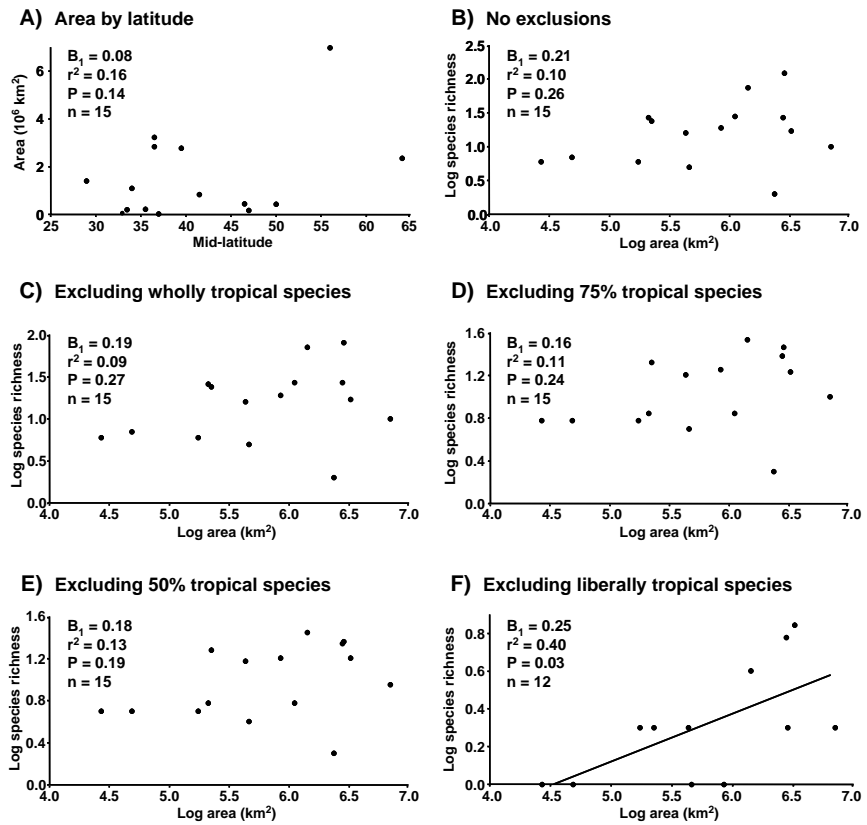
are excluded from estimates of richness, but is non-significant in all other situations, with r^2 ranging from 0.09 to 0.13. At the focal scale of provinces, the relationship is consistently non-significant for exclusions of tropical species by any criterion, with r^2 ranging from 0.02 to 0.09. Ascribing biological importance to the single significant log-log relationship between richness and area for all bats is unwarranted for three reasons: (1) the number of

spurious conclusions of significance that is expected when conducting 10 analyses is 0.5 (1 was observed), (2) the level of significance was not exceptional ($P=0.03$), and (3) the significance of the result is largely associated with the marked reduction in species richness for two of the smallest biomes (South American temperate broadleaf forest and South American evergreen sclerophyllous forest/scrub: when one or both are removed from the analysis, the P

Table 2. Results of regression analyses of log species richness as a function of log area of extratropical biomes and provinces, illustrating the effect of excluding primarily tropical species. Degrees of exclusion are based on the how much of the geographic range of a species is contained within the tropics: wholly tropical species have their entire ranges in the tropics, and liberally tropical species are those for which any part of the range is in the tropics. NA indicates combinations of taxon and degree of exclusion for which sample size is zero.

Scale	All species		Molossidae		Phyllostomidae		Vespertilionidae	
	r^2	P	r^2	P	r^2	P	r^2	P
Biomes								
No exclusions	0.10	0.26	0.21	0.11	0.21	0.26	0.15	0.15
Excluding wholly tropical species	0.09	0.27	0.21	0.12	0.18	0.30	0.15	0.15
Excluding 75% tropical species	0.11	0.24	0.07	0.39	0.20	0.55	0.15	0.15
Excluding 50% tropical species	0.13	0.19	0.07	0.39	0.25	0.32	0.18	0.11
Excluding liberally tropical species	0.40	0.03	NA	NA	NA	NA	0.40	0.03
Provinces								
No exclusions	0.09	0.14	0.15	0.11	0.04	0.57	0.11	0.10
Excluding wholly tropical species	0.09	0.14	0.16	0.11	0.04	0.57	0.11	0.11
Excluding 75% tropical species	0.07	0.20	<0.01	0.99	0.33	0.43	0.09	0.15
Excluding 50% tropical species	0.08	0.16	<0.01	0.99	0.59	0.23	0.10	0.11
Excluding liberally tropical species	0.02	0.59	NA	NA	NA	NA	0.02	0.59

Fig. 3. Graphical assessment of the spillover effect for New World bats and biomes. The relationship between area and mid-latitude (A), as well as the log-log relationship of species richness and area of extra-tropical biomes for all species (B), excluding wholly tropical species (C), excluding species with 75% of their geographic distribution in the tropics (D), excluding species with 50% of their geographic distribution in the tropics (E), and excluding species with any of their geographic distribution in the tropics (F). Regression lines indicate significant relationships at an alpha of 0.05 (Table 2). No distinction was made between northern and southern mid-latitudes in these analyses.



values become non-significant). Parallel analyses that are restricted to phyllostomids, molossid, or vespertilionids (Table 2) generally do not corroborate a spillover effect. More specifically, only 1 of 26 analyses was significant (i.e. vespertilionids excluding liberally defined tropical species, $P=0.03$), which is quite similar to the 1.3 analyses that would be expected on average to appear as significant by chance alone when conducting a suite of independent analyses at an alpha level of 0.05.

Area's signal

The empirical justification for Rosenzweig's (1992, 1995) contention that tropical zones are larger than their extra-tropical counterparts was based on a broad latitudinal delineation of nine zones (i.e. northern tundra, northern boreal, northern temperate, northern subtropical, tropical, southern subtropical, southern temperate, southern boreal and southern tundra). In contrast, Rohde (1997, 1998) recognized five zones (northern polar, northern temperate, tropical, southern temperate and southern polar) and showed that the tropics is neither the largest zone worldwide, nor the largest zone within continents, except for Africa. Effectively, both categorizations, as well as that of Blackburn and Gaston (1997), which

differs only slightly from that of Rosenzweig (1992), are based only on latitudinal limits (i.e. primarily temperature and solar insolation), and do not reflect the importance of water limitations or regional heterogeneity in vegetational formations. Although the subsequent delineation of zones by Ruggiero (1999) was somewhat more sensitive to regional heterogeneity, only the zone classification used by Hawkins and Porter (2001) – based on Whittaker's (1970) schema – reflected a balanced consideration of temperature, precipitation, and regional heterogeneity. Using a worldwide database, they conclusively show that tropical zones are of intermediate size compared to zones at other latitudes. Extra-tropical zones in northern latitudes were largest, and extra-tropical zones in southern latitudes were smallest. Our analyses used a more fine-grain delineation of biomes and provinces within the New World, one that was sensitive to gradients of temperature and moisture, as well as regional heterogeneity (Udvardy 1975). Results corroborated the conclusion that tropical zones are not larger than their extra-tropical counterparts in the Western Hemisphere. Indeed, the areas of biomes or provinces in the New World do not vary with latitude in a systematic fashion (Fig. 2A, 2B). Clearly, the foundational assumption of the geographic area hypothesis has no empirical support in the continental New World at the two ecological scales of our analyses.

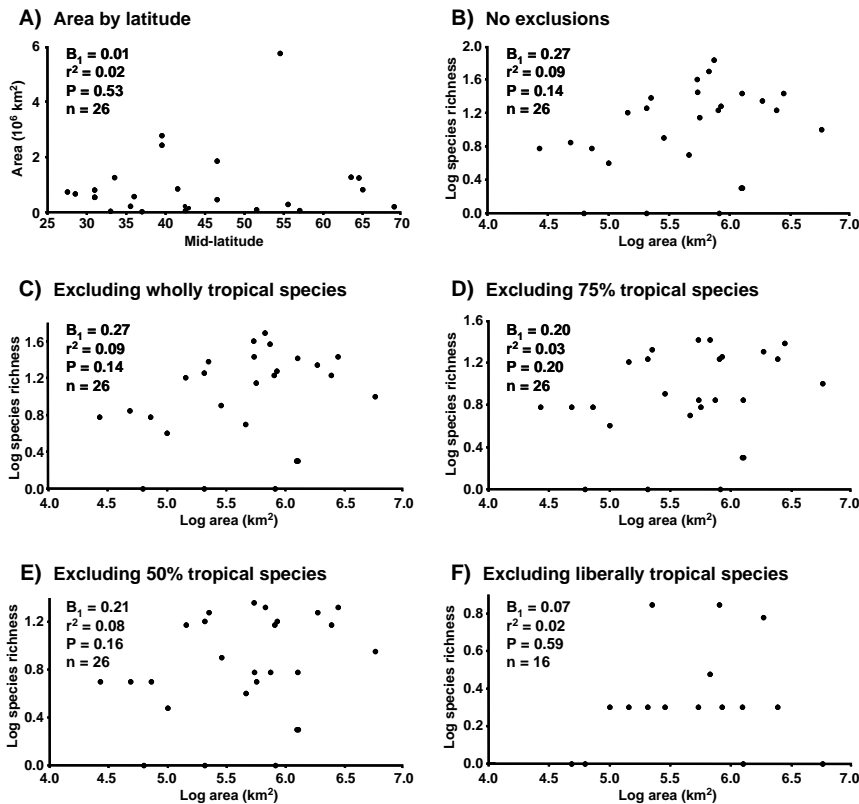


Fig. 4. Graphical assessment of the spillover effect for New World bats and provinces. The relationship between area and mid-latitude (A), as well as the log-log relationship of species richness and area of extra-tropical provinces for all species (B), excluding wholly tropical species (C), excluding species with 75% of their geographic distribution in the tropics (D), excluding species with 50% of their geographic distribution in the tropics (E), and excluding species with any of their geographic distribution in the tropics (F). None of the relationships were significant at an alpha of 0.05 (Table 2). No distinction was made between northern and southern mid-latitudes in these analyses.

Latitude's signal

Despite considerable stochastic variation in the size of ecogeographic zones, the effect of latitude on species richness of those zones in New World bats is quite strong. At the focal scale of provinces ($r^2 = 0.76$, $P < 0.001$) and that of biomes ($r^2 = 0.62$, $P < 0.001$), highly significant linear increases in bat species richness occur toward the equator. This is generally true for the three families of bats when considered separately (r^2 range from 0.76 for molossids in provinces to 0.14 for vespertilionids in provinces), except for the vespertilionids at the focal scale of biomes ($r^2 = 0.03$, $P = 0.357$). Moreover, the proportion of variation in species richness that is related to variation in area is consistently greater at the focal scale of provinces than at the focal scale of biomes. Thus, at the ecological scales of our analyses, variation in area essentially acts as noise, which diminishes the effects of latitude's environmental correlates on species richness. In other scales of analysis, latitude's signal may be so strong that it entirely obfuscates the effects of area. For example, in analyses of the effects of latitudinal band area on mammalian species richness in North America (Kaufman 1994, Kaufman and Willig 1998), the smallest bands (i.e. those toward the equator) have the highest richness and the largest bands (i.e. those toward polar regions) have the lowest richness. Indeed, the effect of latitude is so strong

in this case that it effectively reverses the classical species–area relationship: species richness has a negative correlation with area because area has a positive correlation with latitude, and latitude is the driving factor molding richness (Willig 2000).

Spillover effect

According to Rosenzweig (1992, 1995) and Rosenzweig and Sandlin (1997), the distributions of some tropical species spill over into extra-tropical ecogeographic zones, thereby reducing the strength of the species–area relationship. Of course, this supposition is most relevant to understanding the latitudinal gradient in species richness when tropical zones are larger than their extra-tropical counterparts. Nonetheless, to assess the effects of area on species richness in the context of the geographic area hypothesis, one must compare the strength of the species–area relationship in general to the strength when reducing the extent of analysis to extra-tropical zones and excluding tropical species. Generally, the relationship between richness and area was non-significant regardless of definition of tropical (Table 2) and regardless of taxonomic identity of the focal group of species (i.e. all bats or either of the three most species-rich families). Taken together, the absence of a spillover effect and the absence of a latitudinal

gradient in the area of ecogeographic zones suggest that the geographic area hypothesis is a dysfunctional explanation for the latitudinal gradient in species richness, at least in the New World and most certainly for bats. These results and those of others (Ruggiero 1999, for South American bats and rodents; Fine 2001, for North American trees; and Hawkins and Porter 2001, for terrestrial birds in six biogeographic regions (i.e. Afrotropical, Australasian, Neotropical, Nearctic, Oriental and Palearctic regions); but compare with Blackburn and Gaston 1997, for New World birds) provide strong motivation to remove geographic area from the pantheon of general and viable hypotheses thought to drive the latitudinal gradient in diversity.

Future directions and the diversity of New World bats

To understand the latitudinal gradient in species richness, renewed attention should be directed toward distinguishing the mechanisms that enhance alpha diversity within communities from those that enhance beta diversity among communities at particular latitudes or within ecogeographic regions (Willig et al. 2003a). Indeed, both alpha and beta diversity of bats increase toward the tropics in the New World (Stevens and Willig 2003, Willig et al. 2003b) and contribute to the significant and dramatic increase in species richness of bats in equatorial regions (gamma diversity) in general (Willig and Selcer 1989, Willig and Sandlin 1991). Moreover, this increase in species richness parallels a dramatic increase in the functional diversity as well as in the phenotypic diversity of bats within local communities. Nonetheless, increases in species richness from high to low latitudes alone do not fully account for the rate of increase in functional diversity (Stevens et al. 2004) or phenetic diversity (Stevens et al. 2005) at the community level. Indeed, the markedly distinct distributional characteristics of the three species-rich families of bats in the Western Hemisphere, especially that of the Phyllostomidae, contributes to the rapid increase in diversity that transpires in the subtropics (Stevens 2003, Stevens et al. 2004). More specifically, the Phyllostomidae comprises over half (~145 species) of the New World bat species (Koopman 1993), and is an ecologically diverse family that uniquely comprises the chiropteran representatives of a number of feeding guilds (i.e. sanguivores, frugivores, nectarivores). The family's distribution in the New World is largely tropical and subtropical (Koopman 1982, 1993, Willig and Selcer 1989, Willig and Sandlin 1991). Compared to representatives of other bat families in the New World, phyllostomid species are relatively large, have narrow thermoregulatory requirements, and dietary restrictions that constrain their distributions for physiological rea-

sons to energy-rich and warmer regions of the hemisphere (McNab 1969, 1980, 1986, 1988a, 1988b, Stevens 2003).

In addition, the bounded nature of continental landmasses in the Western Hemisphere enhances the likelihood that stochastic processes predispose latitudinal gradients to peak in equatorial regions because of geometric constraints on the location of range boundaries (Colwell and Hurtt 1994, Lyons and Willig 1997, Willig and Lyons 1998, Colwell et al. 2004). Indeed, the application of an analytical version of the geometric constraints model suggests that much of the variation in bat species richness in the New World (67% to 77% depending on focal group) is accounted for by stochastic processes (Willig and Lyons 1998). Although such a result could be interpreted to mean that chance determines the distributional limits of bat species, it may be interpreted more appropriately to mean that the identity of the factors that limit the northern and southern distributional limits may be taxon-specific. Nonetheless, the random model is biased with respect to the latitudinal gradient of bat species richness: it underestimates tropical richness and overestimates extra-tropical richness. Moreover, the residuals from the model are not related to the continental width (i.e. area). Thus, factors other than area and chance must be acting to produce the observed gradient.

In a recent synthesis concerning diversity gradients, Scheiner and Willig (2005) suggest that any environmental factor that affects the number of individuals in an area will increase richness (i.e. the more individuals hypothesis of Srivastava and Lawton 1998) because of one of three mechanisms (random placement or passive sampling (Coleman 1981, Coleman et al. 1982, Hubbell 2001), local extinction (Preston 1962a, 1962b), or speciation (VanderMeulen et al. 2001)). Indeed, the global increase in incident energy from extra-tropical to tropical regions (Currie 1991, Hawkins et al. 2003, Currie et al. 2004) may be the most parsimonious explanation for the increase in abundance of individuals from extra-tropical to tropical regions, thereby effecting marked deviations between the latitudinal gradient in species richness produced by chance and that observed empirically for New World bats.

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