

The Latitudinal Gradient of Species-Area Relationships for Vascular Plants of North America

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ABSTRACT: The species-area relationship (SAR), describing the increase in species richness with increasing area, and the latitudinal diversity gradient (LDG), describing the decrease in species richness with increasing latitude, are the oldest and most robust patterns in biogeography, yet connections between them remain poorly understood. Here, using 1,742 floras covering the entirety of North America north of Mexico (NAM) and including all of NAM's native species of vascular plants, we show that the slope of the SAR consistently decreases with increasing latitude. This trend is general and holds for subsets of the floras in eastern and western NAM. The southernmost latitudinal quarter of NAM exhibits SARs more than twice as steep as those of the northernmost quarter for both eastern and western regions. This decrease in SAR slope with increasing latitude is consistent with the environmental texture hypothesis and Rapoport's rule, and it suggests that more detailed studies of species endemism in relation to environmental and historical factors will yield significant insights into the underlying causes of SAR and LDG patterns.

Keywords: endemism, environmental texture hypothesis, floristic analysis, Rapoport's rule, species-area curve, species richness.

For all their apparent complexity and diverse histories, large biological assemblages generally obey two biogeographic

rules: they contain more species the closer they are to the equator (Hillebrand 2004) and the larger their area (Rosenzweig 1995; Gotelli 1998). These two patterns, the latitudinal diversity gradient (LDG) and the species-area relationship (SAR), have been well described for over a century (Darwin 1859; in Williams 1964) and remain icons of biogeography despite recent scrutiny (Palmer and White 1994; Crawley and Harral 2001; Willig et al. 2003; Hillebrand 2004; Fridley et al. 2005; Drakare et al. 2006; Hawkins et al. 2006; Mittelbach et al. 2007). However, there remains little consensus about which of the many hypothetical processes underlies such consistent patterns (for reviews, see Pianka 1966; Rohde 1992; Palmer 1994; Rosenzweig 1995; Lomolino 2000; Hillebrand 2004). One common observation thought to contribute to the latitudinal gradient is that species inhabiting temperate and polar regions have larger ranges than tropical species—the so-called Rapoport's rule (Stevens 1989). Rapoport's rule should, in turn, influence SARs because in regions containing species of large ranges, the accumulation of species as area increases should be slower than in regions with higher rates of endemism (Stevens 1989; Arita and Rodríguez 2002). This suggests a connection between LDG and SAR patterns: SARs should be steeper at lower latitudes and decline as the average species range size increases toward the poles (MacArthur 1965, 1969; Lyons and Willig 2002).

As intuitive as a relationship between LDG and SAR patterns may be, very few studies have examined whether SARs vary systematically with latitude. In a large meta-analysis of SAR studies, Drakare et al. (2006) documented a decline in the steepness of SARs with increasing latitude for a data set including a variety of taxa, suggesting that the relationship between LDG and SAR is general. However, other studies (e.g., Connor and McCoy 1979; Martin 1981; Lyons and Willig 2002; Rodríguez and Arita 2004; Sojininen et al. 2007) document conflicting patterns even for the same set of organisms. For example, Connor and McCoy (1979) demonstrated that island SARs bear no relationship to latitude for birds, a conclusion examined and rejected by Martin (1981). In contrast to the meta-analysis of Drakare et al. (2006), Storch et al. (2005) dem-

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onstrated that the slope of SARs for birds is shallower in areas with higher levels of available energy, suggesting that higher energy availability nearer the equator should lead to shallower tropical SARs. Soininen et al. (2007) reported that the slope of SAR increases with latitude for sample units $>1 \text{ km}^2$. Koleff et al. (2003) concluded that very little is known about range distributions and regional species turnover in relation to latitude. Thus, although there are good reasons to believe the latitudinal gradient exists in part because smaller species ranges beget steeper SARs near the equator, current evidence is insufficient to conclude that this phenomenon exists and contributes to LDG for a wide variety of organisms.

Vascular plants of North America have been a continual testing ground for latitudinal gradient theories (Monk 1967; Glenn-Lewin 1977; Stevens 1989; Currie 1991) and demonstrate a clear decrease in species diversity toward the poles (Rosenzweig 1995, Qian 1999; Fridley et al. 2006*b*; but see Stohlgren et al. 2005). Although it has been hypothesized that the rate of species accumulation with increasing area decreases northward (Fridley et al. 2005; Palmer 2006), we know of no studies relating SARs to latitude for North American plants. North America north of Mexico (NAM) is a suitable testing ground for relationships between LDG and SAR for several reasons: it is one of the few continents that have a wide longitudinal span from relatively low (ca. 25°) to high latitudes, enabling examination of SARs at a large spatial extent across latitudes; eastern and western boundaries are delimited by oceans, eliminating possible biases resulting from different surrounding areas (water vs. land) in different latitudinal zones; the two major mountain systems are oriented along a N-S axis, reducing differences in topography at different latitudes; and floras of NAM are well documented at multiple scales for the full latitudinal extent.

In this study our objective is to test whether the steepness of SARs decreases with increasing latitude, reflecting greater endemism and smaller ranges at lower latitudes. Our study is based on a comprehensive database of 1,742 floras including all ca. 16,200 species and hybrids of vascular plants native to NAM. We model the log-log slope of species richness and area—or z value (Rosenzweig 1995; Fridley et al. 2005)—as a function of latitude for a data set of all 1,742 floras and for subsets based on broad latitudinal and longitudinal domains. In addition, we test the prediction of Storch et al. (2005) that the slope of SARs is shallower in areas with higher levels of available energy.

Methods

Floristic Data set

A total of 1,742 floras of NAM were included in our study (fig. 1), derived from a compilation of state and provincial

data, the FloraS of North America database, and additional floristic literature (see app. A in the online edition of the *American Naturalist* for a list of the literature and other sources from which the data used in this study were compiled; see Withers et al. 1998; Palmer 2005; 2006; <http://botany.okstate.edu/floras/> for details about FloraS). Data from Kartesz (1999) were used to produce the species checklist of each of the states/provinces except for California, Texas, and Ontario (see below). Because the native or introduced status of each species in Kartesz's (1999) work is defined based on the nativity of a species to the entirety of Canada, the United States (including Hawaii, Puerto Rico, and U.S. Virgin Islands), and Greenland, some species native to Hawaii, Puerto Rico, and/or U.S. Virgin Islands but exotic to NAM are treated as natives. We exclude those species that are treated as native by Kartesz (1999) but are exotic to NAM.

We divided California and Ontario into southern and northern parts to make boundaries of latitudinal zones more consistent across longitudes. The division through California was placed on the southern boundaries of the following counties: Mono, Tuolumne, Stanislaus, Alameda, and San Francisco; the division through Ontario was placed on the southern boundaries of Manitoulin District, Nipissing District, Parry Sound District, and Renfrew County. Species checklists were compiled according to CalFlora (<http://www.calflora.org>) for the two parts of California and were based on an Ontario plant database (M. Oldham, unpublished data) for the two parts of Ontario. We divided Texas into six sections: three are areas 5, 7, and 10 of Hatch et al. (1990), and the other three are combinations of the rest of the areas of Texas studied by Hatch et al. (one section including areas 1, 3, and 4; one section including areas 2 and 6; and one section including areas 8 and 9). A species checklist for each section was compiled from Hatch et al. (1990). We added to these lists 1,119 floras of the FloraS of North America database (Withers et al. 1998; Palmer 2005), excluding those that are for states/provinces or larger units; those that exclusively describe wetlands, ponds, high elevations, or mountaintops; and those that were published before 1950. We added 115 additional floras of vascular plants from the literature published or originally compiled after 1950 and from aggregated county species lists. To fill a large data gap in the region of the Canadian eastern Arctic, we included one comprehensive pre-1950 flora (Polunin 1940), from which species numbers for nine arctic areas were counted.

Zones of Latitude and Longitude

We divided NAM into four latitudinal zones (fig. 1). Zones 3 and 4 were separated by 60°N latitude and the northern

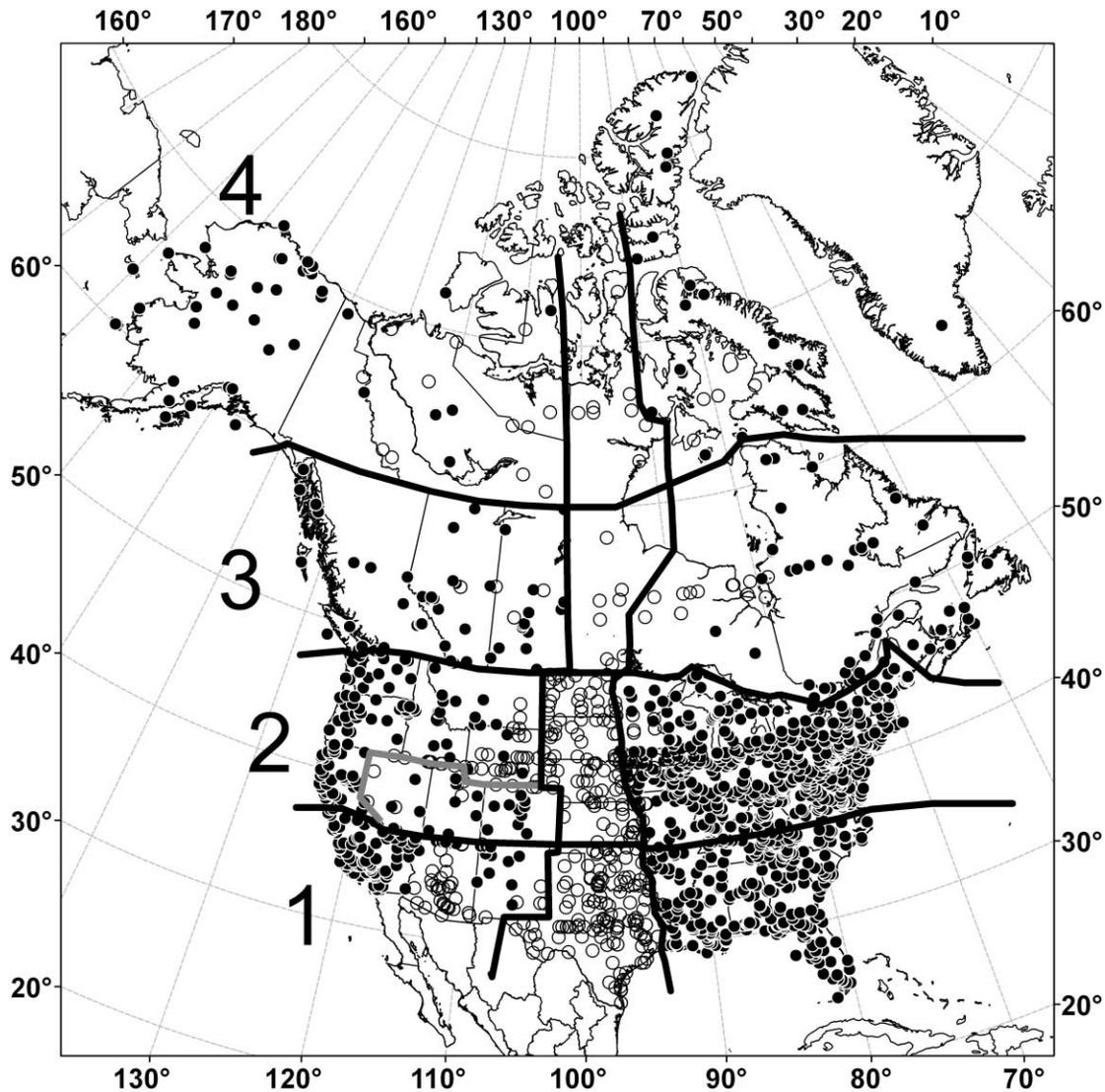


Figure 1: Geographic midpoints of the 1,742 floras from the United States, Canada, and Greenland used in this study. Filled circles indicate floras of eight regions in eastern and western North America. Open circles indicate floras used in the analyses for all of North America north of Mexico but not for eastern or western regions because they are not constrained to any of the regions. The strip lying between the two solid vertical lines separates eastern and western North America. The three solid horizontal lines separate the four numbered latitudinal zones. Lines separating regions within longitudinal zones are the same lines separating latitudinal zones except for the line separating the two southern regions in western North America, which is a solid gray line.

tip of Quebec; zones 2 and 3 were separated by roughly 50°N latitude and the tip of Maine; and zones 1 and 2 were separated by the division through California and 37°N latitude in the west (dividing Arizona and Utah, New Mexico and Colorado, Oklahoma and Kansas) and by the northern boundaries of Arkansas, Tennessee, and North Carolina in the east. We aggregated contiguous state-level units within a latitudinal zone to generate larger floras (i.e., two states, three states, ..., all states in a latitudinal

zone). We avoided generating elongated floras, such as Tennessee plus North Carolina, for those aggregated floras that do not occupy the entire width of the latitudinal zone. In total, 516 state-level or larger (aggregated) floras were generated. Twenty-two of these floras were not assigned to any latitudinal zone because they are located in more than one zone.

We also grouped floras into western and eastern longitudinal zones (fig. 1). Those floras that are partly or fully

located in the middle strip of the continent between the two longitudinal zones were excluded (*open symbols*, fig. 1). As a result, 1,366 floras were assigned to one of the longitudinal zones (974 for the eastern zone, 392 for the western zone). To perform the same latitudinal SAR analyses for these longitudinal subregions, we divided each into the four latitudinal zones described above except for the boundary between the two southern regions of the western zone, which were separated by the northern boundaries of southern California, Nevada, Utah, and Colorado, to minimize the difference in area between them. The largest sample in each of the eight regions includes the entirety of the region. Summary statistics for floras of each region are listed in table 1.

Climate Data

Temperature and potential evapotranspiration (PET) have been widely considered measures of ambient energy and related to large-scale species richness (e.g., Currie 1991; Rodríguez et al. 2005; Hawkins et al. 2003). We obtained temperature data from the CRU global climate data set developed by the Climatic Research Unit (New et al. 1999) and PET data from the global evapotranspiration and water balance data set (Ahn and Tateishi 1994). Both data sets were available at a spatial resolution of half-degree squares of latitude and longitude. A total of 11,671 half-degree squares are located in our study area. We extracted mean annual temperature and annual PET for each square, assigned each to a latitudinal zone or region according to its midpoint location, and calculated the mean values of annual temperature and annual PET for each of the four latitude zones and the eight regions.

Statistical Analyses

We examined the relationship between SAR and latitude for NAM vascular plants in two ways. First, we fit a linear least squares regression model of the form $\log S = b_0 + b_1 \times \log A + b_2 \times \text{latitude} + b_3 \times \text{latitude} \times \log A$ to examine the interaction of latitude and $\log A$, where $\log A$ and $\log S$ are \log_{10} -transformed flora area and species richness, respectively. A negative coefficient for b_3 means the slope of the SAR decreases with increasing latitude. Second, we fit the model to three separate data sets: all of NAM, eastern NAM, and western NAM. We then compared z values of the model $\log S = c + z \times \log A$ between four latitudinal zones for all of NAM, four latitudinal zones in eastern NAM, and four latitudinal zones in western NAM. The log-transformed power model is among the simplest and most commonly used SAR functions over the range of spatial scales in our study (Arrhenius 1921; Preston 1960; Williams 1964; Rosenzweig 1995; Hubbell 2001; Fridley et al. 2005; Drakare et al. 2006). Although several other SAR models have been explored in the literature over the past several decades (e.g., Connor and McCoy 1979; He and Legendre 1996; Tjørve 2003), SARs generally fit a straight line in log-log space over continental areas that span from ca. 1 ha to more than 1,000,000 ha (Rosenzweig 1995; Fridley et al. 2005, 2006a; see below for areas beyond this threshold) and have the desirable property of using the simple regression slope (z) as a measure of the rate of species accumulation with increasing area. We also note that parameter estimates from our SAR models are derived from statistically nonindependent data, as is the case for all SAR studies (Gotelli and Colwell 2001; Colwell et al. 2004). Although parameter estimates themselves are unbiased, statistical inference from these estimates is problematic (Colwell et al. 2004). For the full regression models including latitude \times area interaction

Table 1: Summary statistics for floras in latitudinal bands (zones 1–4) and regions in eastern (E1–E4) and western (W1–W4) North America north of Mexico

Zone or region	N	Area (ha)				Number of species			
		Minimum	Maximum	Mean	SD	Minimum	Maximum	Mean	SD
Zone 1	532	8.5	2.8×10^8	1.1×10^7	3.4×10^7	50	12,221	1,168.4	1,691.2
Zone 2	971	5.0	4.9×10^8	3.3×10^7	7.1×10^7	56	11,199	1,706.3	1,953.3
Zone 3	130	5.4	5.4×10^8	7.6×10^7	1.3×10^8	52	3,867	1,038.8	1,007.8
Zone 4	87	8.5	5.2×10^8	6.5×10^7	1.2×10^8	49	1,739	454.7	461.3
E1	277	8.5	8.5×10^7	5.2×10^6	1.5×10^7	53	4,879	1,040.5	1,117.2
E2	623	5.0	1.9×10^8	1.3×10^7	2.9×10^7	56	5,023	1,221.8	1,226.5
E3	53	1.4×10	2.7×10^8	5.1×10^7	8.6×10^7	52	2,385	948.4	788.6
E4	19	4.1×10^3	1.1×10^8	1.3×10^7	2.5×10^7	59	497	162.3	115.3
W1	128	1.6×10	1.6×10^8	1.6×10^7	3.6×10^7	63	8,222	1,518.7	2,112.2
W2	128	1.1×10	1.4×10^8	1.3×10^7	3.2×10^7	61	6,898	1,217.5	1,613.2
W3	50	8.9	2.2×10^8	1.6×10^7	4.4×10^7	65	2,738	531.7	646.5
W4	43	8.5	3.3×10^8	2.7×10^7	6.9×10^7	78	1,603	412.9	391.0

terms, we report measures of statistical significance (P values; table 2), with the realization that these estimates reflect inflated Type I error (Diniz-Filho et al. 2003; Hurlbert 2004). To remedy this problem, we followed previous authors (e.g., Francis and Currie [2003]; Hurlbert [2004]) in comparing probabilities of a model with probabilities calculated based on a very small number of samples used to parameterize the model. We found that all of the models with their probabilities of statistic inference reported in this study remained significant at $P < .05$ even if fewer than 5% of the floras included in each model were statistically independent.

We were aware of three potential biases inherent in a simple application of linear least squares to the structure of our data sets. First, we were concerned that errors in the estimate of species richness from floras are not distributed symmetrically about the mean, as assumed in linear least squares regression, but are biased toward undercounts (Palmer 1995). Although this should be a general concern of all biogeographic studies of species richness where perfect species detection is a challenge (Palmer et al. 2002; Fridley et al. 2006b; Moerman and Estabrook 2006), very few SAR studies consider the implications of nonnormal error distributions in model fitting (Gotelli and Colwell 2001; Cam et al. 2002). In our study, biased undercounts could provide a mischaracterization of true SARs if undercounts are more likely in floras of certain sizes. Furthermore, we suspect that residuals of SARs may be asymmetrical for ecological reasons (e.g., extreme environments) in addition to undercount biases. To account for these possibilities, we estimated upper-envelope SAR slopes via quantile regression with the “quantreg” statistical package for R (Koenker 2006), which implements the modified Barrodale and Roberts algorithm described by Koenker and d’Orey (1987). Our desire was to estimate a slope quantile representing the upper envelope of the data, but it was not clear which upper quantile to use or whether our analysis would be sensitive to use of a specific quantile. We therefore estimated both ninetieth and ninety-fifth regression quantiles and tested whether slope coefficients were different using an F -like statistic described by Koenker and Basset (1982). Statistical analyses were performed in the R statistical package (R Development Core Team 2006).

Second, the sample size of floras tends to decrease with increasing latitude (fig. 1). This tendency may bias the pattern of decreasing z values with increasing latitude because each latitudinal zone or region includes more floras from its southern part than its northern part. Because larger floras include a larger proportion of the latitudinal range of a zone or region, this bias is enhanced toward smaller floras, thus causing a potential spurious decrease in z . We therefore conducted an additional set of analyses

Table 2: Least squares regression statistics for predictive models of \log_{10} -transformed species richness ($\log S$) regressed on \log_{10} -transformed area ($\log A$), latitude, and their interaction, for all of North America north of Mexico and eastern and western subsets

Effect	Coefficient	Partial r^2	P
North America:			
Intercept	1.6653		<.00001
Log A	.3542	.309	<.00001
Latitude	.0034	.002	.05363
Latitude \times log A	-.0035	.070	<.00001
Eastern North America:			
Intercept	1.5479		<.00001
Log A	.3828	.261	<.00001
Latitude	.0097	.011	.00086
Latitude \times log A	-.0047	.082	<.00001
Western North America:			
Intercept	.9924		<.00001
Log A	.4688	.515	<.00001
Latitude	.0133	.061	<.00001
Latitude \times log A	-.0052	.209	<.00001

Note: The effect of area decreases with increasing latitude for all three data sets. See figure 1 for geographic distribution of floras. Sample size (n) and coefficient of determination (r^2) are, respectively, 1,742 and 0.821 for the whole of North America; 972 and 0.803 for eastern North America; and 408 and 0.865 for western North America.

that used only those floras whose midpoint latitudes fell into the central 20% of the latitudinal range of a zone or region. Because the midpoints of all sample units within a zone and region fell into this narrow latitudinal zone, we believe a SAR resulting from these sample units for each zone or region is unbiased in terms of latitude. Because this sampling bias was not apparent in the four northernmost regions and because the subsets of floras selected in this way for the two northern zones were not large enough to make reliable statistic analyses, we resampled floras for only the two southern zones and their four regions.

Third, we were aware that SARs that include very large areas (approaching the size of whole land masses) deviate from the linear log-log functional form expectation. Several well-known studies (e.g., Preston 1962; Williams 1964; Rosenzweig 1995) have demonstrated the rapid increase in SAR slope as areas extend from single biotic provinces to global richness estimates, and SARs that span these discontinuities should not be expected to follow strict log-log linear behavior (Hubbell 2001; Fridley et al. 2005). Preliminary investigation of SARs from the floras data set presented here suggested that such an upturn is apparent around 100,000,000 ha (evident in fig. 2), an area exceeded by 197 of the 1,742 floras in our data set. To ensure that inclusion of these megascale floras did not influence our conclusions on latitudinal patterns of log-log linear esti-

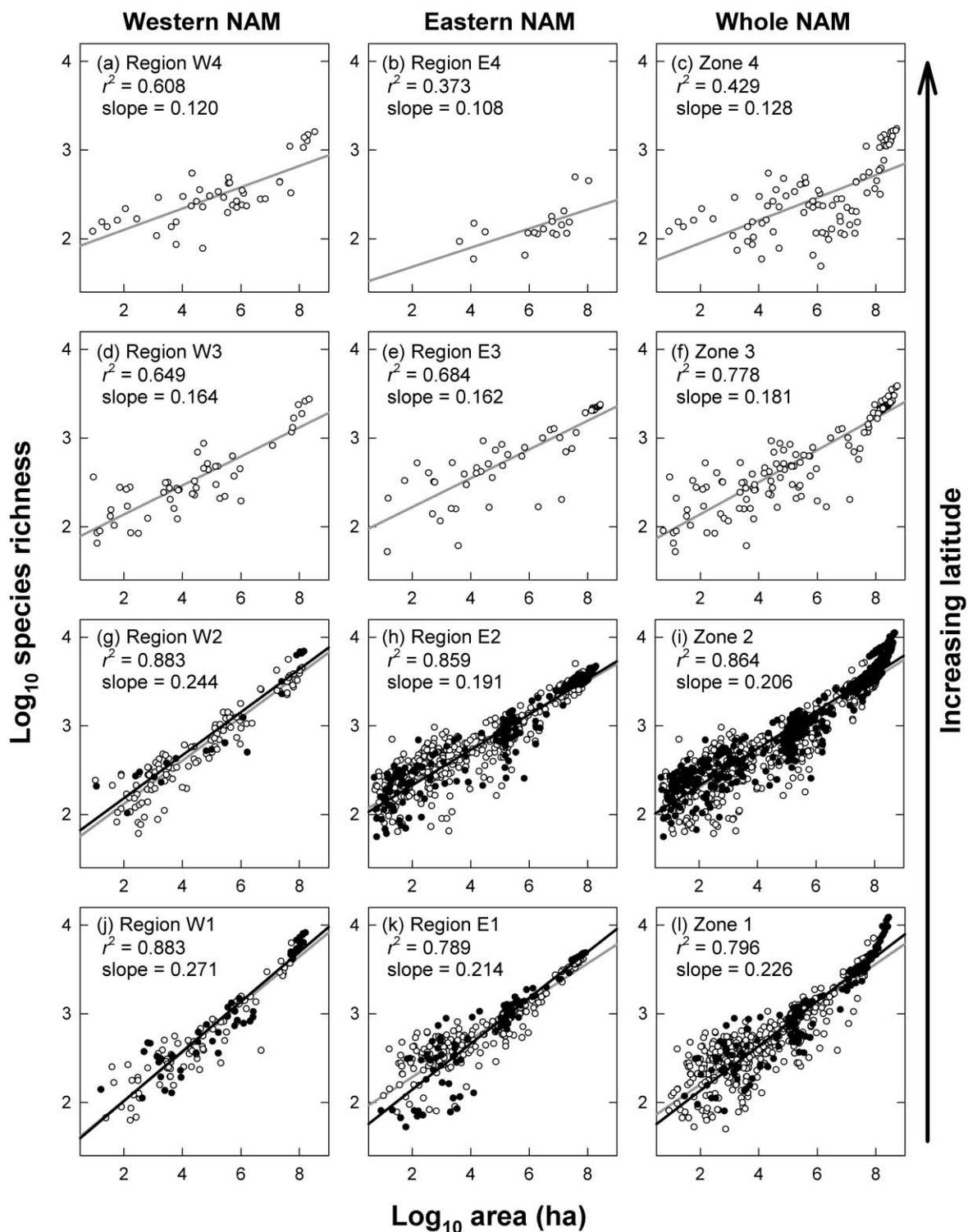


Figure 2: Species-area relationships for vascular plant floras of four latitudinal bands of North America north of Mexico (NAM; see fig. 1). Filled circles in *g-l* represent floras whose centers are within the central 20% of the latitudinal ranges of a zone or region in which they are located. The gray line, coefficient of determination (r^2), and slope result from linear least squares regression using both open and filled circles; the black line in *g-l* results from linear least squares regression using only filled circles.

mates of z , we conducted an additional SAR analysis for latitudinal band subsets that omitted these 197 floras.

Results

The slope, z , of the overall SAR decreased with latitude, as shown by significant negative area \times latitude interaction terms in models of floristic richness for all of North America and eastern and western data subsets (table 2). Partial coefficients of determination were higher for the interaction than for latitude by one or two orders of magnitude, depending on data set (table 2), indicating the explanatory value of the interaction. When the data set for the whole of North America was used, the interaction tended to weaken the main effect of latitude. The magnitude of the area \times latitude interaction (-0.0035) in the data set for all of North America was lower than in data sets for eastern (-0.0047) and western (-0.0052) NAM. When those floras in zones 1 and 2 whose mid-latitudes do not fall into the central 20% range of a zone or region were excluded, the slope of the interaction was -0.0035 ($n = 867$, $r^2 = 0.853$) for all of NAM, -0.0064 for eastern NAM ($n = 370$, $r^2 = 0.829$), and -0.0052 for western NAM ($n = 162$, $r^2 = 0.851$). When the data were reanalyzed with the 197 largest floras excluded, the magnitude of the area \times latitude interaction remained lower for the entirety of NAM (slope = -0.0045 , $r^2 = 0.0785$) than for the eastern and western zones, but eastern and western NAM had comparable magnitudes of area \times latitude interaction (slope = -0.0056 , $r^2 = 0.795$ for eastern NAM; slope = -0.0054 , $r^2 = 0.0822$ for western NAM).

In separate SAR models fitted individually by latitudinal zone, z values again consistently declined with increasing latitude (figs. 2, 3), regardless of the type of regression used. For all of North America, z values decreased from 0.23 in zone 1 to 0.13 in zone 4; similar decreases from low to high latitudinal zones were seen for eastern NAM (0.22 to 0.11) and western NAM (0.27 to 0.12). Slopes of upper SAR envelopes estimated with quantile regression were often lower than those of least squares (fig. 3) but showed overall decline with increasing latitude, regardless of data set. On two occasions, ANOVA contrasts indicated significantly different slope estimates for ninetieth and ninety-fifth quantiles: zone 2 for NAM had a ninety-fifth-quantile slope of 0.198, significantly higher than the ninetieth-quantile slope of 0.187 (fig. 3; $P < .01$); this contrast also held for eastern NAM zone 2 (although the ninety-fifth-quantile slope was 0.163, significantly lower than the ninetieth-quantile slope of 0.168). However, in both cases, the overall pattern of z value decline with latitude held for both ninetieth- and ninety-fifth-quantile slopes.

When those floras in Zones 1 and 2 whose midlatitudes

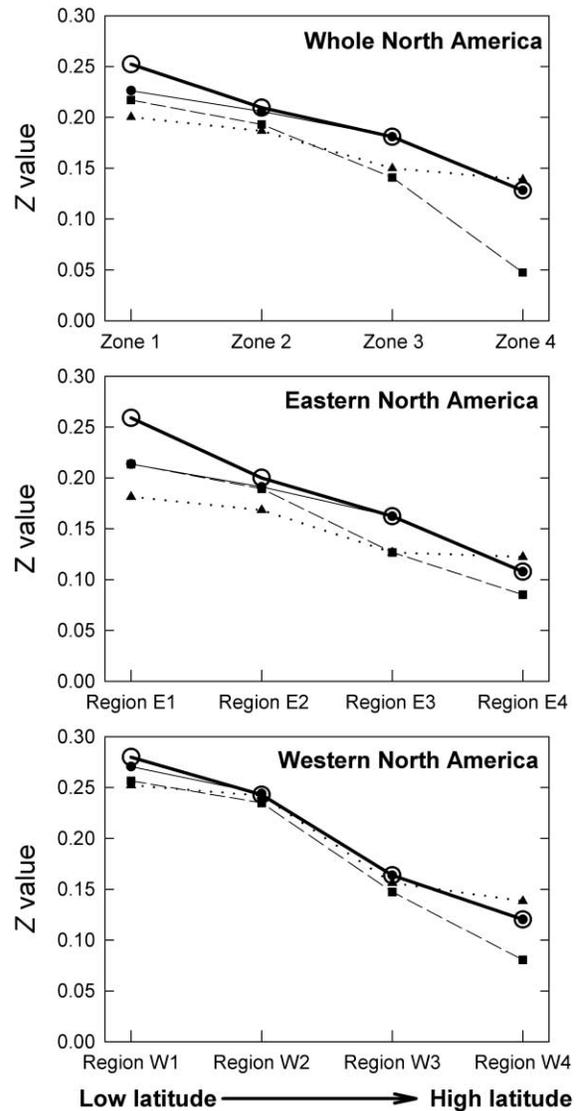


Figure 3: Decline in species-area relationship z values from low to high latitudinal zones and regions (see fig. 1) for whole, eastern, and western North America. Solid thin lines with filled circles represent linear least squares regressions using all floras in a zone or region, dotted lines with filled triangles represent estimates of ninetieth-quantile regressions, dashed lines with filled squares represent least squares regressions omitting floras greater than 100,000,000 ha, and solid thick lines with open circles represent linear least squares regressions omitting floras in the two southern zones whose centers are outside of the central 20% of the latitudinal ranges of a zone or region in which they are located.

do not fall into the central 20% range of a zone or region were excluded, the slope of the log-log relationship between area and species richness was 0.252 and 0.210, respectively, for zone 1 ($n = 150$, $r^2 = 0.869$) and zone 2 ($n = 500$, $r^2 = 0.908$); 0.259 and 0.200 for the southernmost ($n = 88$, $r^2 = 0.820$) and second southernmost

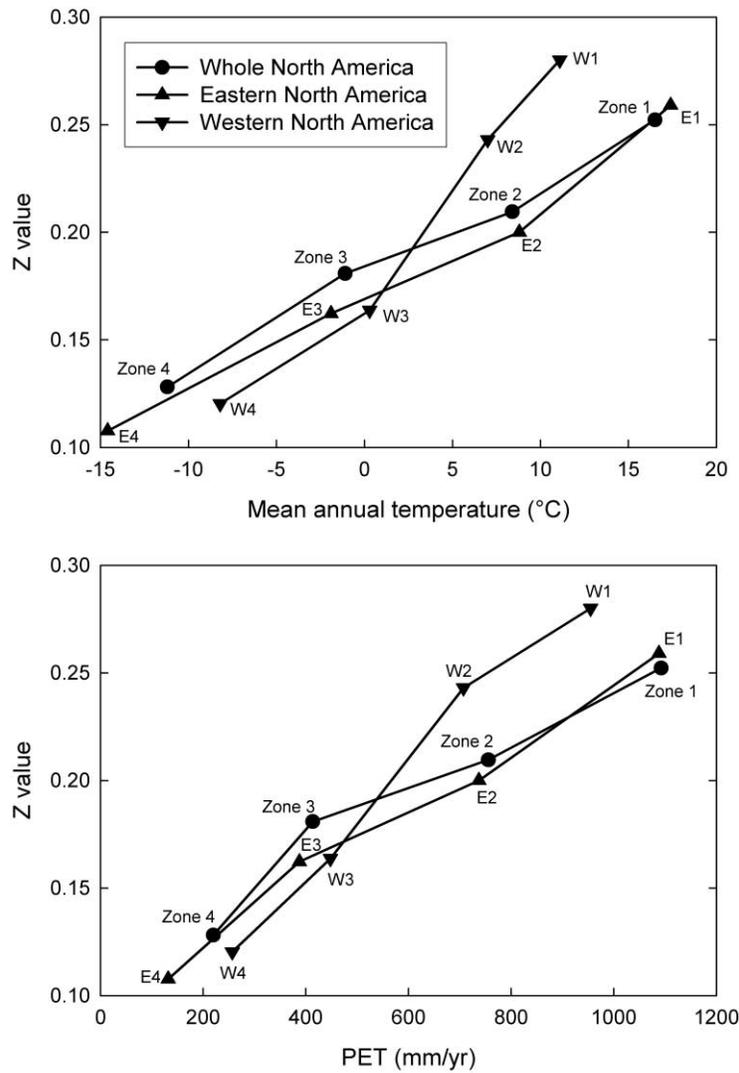


Figure 4: The increase in species-area relationship *z* values (*top*) from low to high temperature and (*bottom*) from low to high potential evapotranspiration (PET) for whole, eastern, and western North America. Temperature and PET values for each data point are the averages of all half-degree latitude-longitude squares within each of latitudinal bands (zones 1–4) or regions in eastern (E1–E4) and western (W1–W4) North America north of Mexico (see fig. 1). For the two southern zones and their regions, *z* values were calculated using those sample units whose centers were located in the central 20% of the latitudinal ranges of a zone or region.

regions ($n = 210, r^2 = 0.900$) in eastern NAM; and 0.280 and 0.243 for the southernmost ($n = 49, r^2 = 0.894$) and second southernmost regions ($n = 20, r^2 = 0.892$) in western NAM. In all regressions, the slopes became steeper and area explained more variance in species richness, compared with the regressions reported previously that used all floras in a zone or region.

The decrease in *z* value with increasing latitude was accentuated when the largest floras (above 100,000,000 ha) were removed from SAR estimates within latitudinal bands (fig. 3). This was primarily the result of strikingly low *z*

value estimates for regions in zone 4 when the largest floras were removed: *z* values changed from 0.13 to 0.05 for zone 4, from 0.12 to 0.08 for the western region of zone 4 (W4), and from 0.11 to 0.09 for the eastern region of zone 4 (E4).

We related *z* values to mean values of mean annual temperature and annual PET for each region and zone (fig. 4). As expected, *z* values increased monotonically with increasing temperature and PET, at a rate faster for western North America. These results are consistent with those reported in figure 3.

Discussion

The connection of SAR and LDG patterns is an essential component of the growing assessment of global biodiversity patterns and their contribution to biogeography theory (Drakare et al. 2006), but few studies have examined this relationship in any detail for a large taxonomic group. Our study, based on 1,742 floras, including all known species of vascular plants in North America north of Mexico and covering a wide range of latitudes (from 25° to 84°), is the first attempt to examine the SAR-LDG relationship for plants at a continental scale. Our study provides clear evidence that SAR slopes decrease consistently from low to high latitudes across longitudinal zones. A full range of z values of SARs for vascular plants in the northern latitudes of the New World may be estimated by combining z values reported in this study with one estimated z value (0.33) for Central America (Kier et al. 2005) and one (0.34) for South America north of approximately the equator (H. Qian, unpublished data). Although floras for high latitudes (zones 3 and 4) were not as well represented as those for low latitudes because they are rarely documented, it is unlikely that the relatively poor representation of high-latitude floras produced the decrease in z value with increasing latitude in our study, given the extreme disparity in large-scale richness between low and high latitudes (nearly an order of magnitude). Furthermore, estimated z values for the two northernmost regions in this study (i.e. 0.11 for E4, 0.12 for W4) are comparable with those reported by Malyshev (1991) for high-latitude regions in Eurasia ($z = 0.102$ for Siberian taiga region, $z = 0.106$ for Putorana, $z = 0.084$ for Arctic of eastern Europe).

Our finding that steeper SARs occur at lower latitudes is consistent with that of some previous studies of individual taxa (e.g., Rodríguez and Arita 2004, for North American mammals), and with meta-analyses of Martin (1981) and Drakare et al. (2006). Our results contrast with those of Lyons and Willig (1999, 2002), who found that z values for New World bats and marsupials increased from the tropics to the poles. However, differences in species pools (they used a small species pool with only 82 species of marsupials and 244 bats in the entirety of North and South America, in contrast to >16,200 species and hybrids of vascular plants in North America) may help explain the inconsistency. Our finding also conflicts with that of Soininen et al. (2007), who demonstrated that the z values increase slightly but nonsignificantly with increasing latitude for sample units >1 km². We suspect that Soininen et al. (2007) failed to detect a negative trend because of the separate calculation of z at two spatial scales and the combination of different taxonomic groups on different continents.

Our results show a dramatic increase of z values toward

areas with high energy measured by temperature and potential evapotranspiration. This finding contrasts with that of Storch et al. (2005), who found that SAR z values are lower in areas of higher energy availability and predicted that z values should generally increase from the tropics to the poles because the spatial turnover of populations decreases with increasing energy availability. The findings of Rodríguez and Arita (2004) as well as Drakare et al.'s (2006) meta-analysis also do not agree with this prediction. Storch et al. (2005) reasoned that southern parts of North America are considerably drier and have lower available energy than more northern areas, and they attributed the decreasing z values toward high latitudes reported by Rodríguez and Arita (2004) to lower energy and water availability in southern latitudes. However, climate data do not support this reasoning; available energy (measured as mean annual temperature and annual PET) monotonically decreases from low to high latitudes in North America, and southern North America is not drier than northern North America in general (fig. B1 in the online edition of the *American Naturalist*; Qian and Ricklefs 1999). The consistency in z value decline with increasing latitude and increase with increasing energy that is reported here for both mesic eastern North America and the drier western North America (particularly in zones 1 and 2) suggests that Storch et al.'s hypothesis cannot account for SAR patterns in North America.

The decrease of z values with increasing latitude suggests that species in higher latitudes have wider geographic ranges, a phenomenon consistent with Rapoport's rule (Stevens 1989). The pattern of z values decreasing with increasing latitude is also consistent with the widely held notion that β diversity increases toward the tropics (Cody 2001; Koleff et al. 2003; Rodríguez and Arita 2004; Qian and Ricklefs 2007). This in part shifts scientific interest in LDG to phenomena of range size and endemism rather than species diversity per se; that is, why should species at lower latitudes have smaller ranges (Dobzhansky 1950; Janzen 1967; Whittaker 1972; Stevens 1989)? Probable explanations for decreasing z values with increasing latitude may involve both environmental and historical considerations, as elaborated below.

Environmental Considerations

There is a necessary link between the geometry of environmental heterogeneity and patterns of endemism and SARs. According to the environmental texture hypothesis (Palmer 2007), the SAR slope is determined largely by the rate at which new environments are encountered as a function of scale; this rate will vary dramatically (and perhaps predictably) as a function of geographical location (see Nekola and White 1999). Broad-scale substrate heteroge-

neity is more pronounced in southern North America than in the ancient granitic shield of much of Canada. The role of edaphic heterogeneity is particularly apparent in southwest North America, where a large number of endemic species are restricted to specialized habitats at different locales (Raven 1977). This region (W1) exhibited the steepest SAR z value in our study and has long been associated with high rates of endemism stemming from the Tertiary uplift of the Rocky Mountains and the associated increasing aridity (Stebbins 1952; Raven 1977; Hickman 1993; Qian 2001). Qian (2001) reported that of the 987 endemic genera of vascular plants in North America, 60% are restricted to the western half of the continent, and 78% of these western North American endemic genera are further restricted to the southwest. Thus, endemism, combined with the geometry of relevant environmental factors, can lead to variation in SARs.

Historical Considerations

The occurrence of larger species ranges in northern North America may also be due to more recent historical events and varying dispersal abilities of northern and southern taxa. Because the northern part of North America was covered by ice sheets during Quaternary glaciations, species currently distributed in North American high latitudes were dispersed from southern latitudes of the continent and/or other ice-free areas of the northern hemisphere. Thus, patterns of current ranges of most species in high latitudes probably resulted from the dispersal abilities and ecological requirements of these species rather than differential speciation events. Morin and Chuine (2006) found that species with smaller and lighter seeds tend to have larger ranges. There is a profound latitudinal gradient in seed size (Moles et al. 2007), which is likely to be inversely correlated with dispersal abilities. Thus, it is reasonable to suppose that a latitudinal gradient in z could result from a latitudinal gradient in dispersal abilities.

Pollen data and simulated plant distributions showed that boreal tree species (e.g., *Picea* spp.) were widely distributed south of ice sheets across the range of longitudes from coast to coast in North America 21,000 years BP (Bartlein et al. 1998). Because of the niche conservatism of plant (Qian and Ricklefs 2004) and animal taxa (Hawkins et al. 2006), many plant species now widely distributed in boreal forests may also be widely distributed in boreal forests located in more southern latitudes during or even before glacial periods. This suggests that a low rate of species turnover and thus low z value of SAR in the boreal biome may have existed before the Last Glacial Maximum.

Nonlinearity of the SAR

Very large areas (approaching the size of the largest floras in our data set) exhibit accelerated rates of species accumulation compared with smaller floras, a pattern that is well established in the SAR literature (Preston 1962; Williams 1964; Rosenzweig 1995; Hubbell 2001; Fridley et al. 2005). For the data we present in figure 2, there is a clear departure from linearity as area approaches 100,000,000 ha (8 \log_{10} units), and z values were greater for data sets that contained these largest floras (fig. 3). Although omission of these larger floras did not influence the general pattern of z value decline with increasing latitude, we acknowledge that a full description of SARs for North America will not be complete until such nonlinearities are fully explored mechanistically (Fridley et al. 2005). If the range of areas reported in this study were extended to include data points for the whole of North America north of Mexico (having 16,226 species and hybrids, according to Qian and Ricklefs [2006]; $\log S = 4.21$, $\log A$ [ha] = 9.28) and the whole ice-free land area of the globe (having 260,140 species, according to Maberley [1997]; $\log S = 5.42$, $\log A$ [ha] = 10.12), the nonlinear acceleration of z values at megascales would be enhanced even further. Future research should establish area thresholds where such nonlinearities occur and link them to environmental (Palmer 2007) or dispersal-based mechanisms (Hubbell 2001). Nonetheless, for the range of scales that do conform to the linear log-log SAR model, our study demonstrates that SARs depend fundamentally on latitude.

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