

Latitudinal Gradients of Biodiversity: Patterns, Processes, and Prospects

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This is an update of M.R. Willig, S.J. Presley, Latitudinal Gradients of Biodiversity☆, Reference Module in Life Sciences, Elsevier, 2017, ISBN 9780128096338, <https://doi.org/10.1016/B978-0-12-809633-8.02174-9>.

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Abstract

The gradient of increasing species richness with decreasing latitude is one of the most well-established patterns in macroecology. The gradient is pervasive in time and space, and pertains to all major taxa. Many ecological and evolutionary mechanisms have been hypothesized to cause the gradient; it is likely that a combination of mechanisms operating over long time frames explain these gradients, with the relative importance of particular mechanisms contingent on taxon or geographic setting. Recent research suggests that other components of taxonomic biodiversity (e.g., species evenness and dominance) do not evince a latitudinal gradient. Latitudinal gradients in functional, phenetic, and phylogenetic biodiversity are strong and are not wholly a product of variation in species richness.

Glossary

α -component of biodiversity The biodiversity of species, often estimated from taxonomic, functional, or phylogenetic perspectives, within a local community or site.

β -component of biodiversity The degree of change in taxonomic, functional, or phylogenetic composition among communities or sites along a gradient or within a larger area.

Biodiversity A multidimensional concept embodying various dimensions (e.g., taxonomic, functional, phylogenetic, and genetic) that characterize variability of the biota in time or space.

Functional biodiversity A characterization of a biota based on variability in ecological attributes among species, providing a mechanistic link to ecosystem resistance, resilience, and functioning.

γ -component of biodiversity The biodiversity of species, often estimated from taxonomic, functional, or phylogenetic perspectives, in a larger area as a consequence of both α - and β -components of biodiversity.

Latitudinal gradient A gradual change in a characteristic of interest (e.g., species richness, phylogenetic biodiversity) with a gradual change in latitude; a gradient is well defined if it adheres to a particular mathematical relationship.

Mid-domain effect A gradient wherein species richness increases symmetrically from the extremes to the middle of a region as a consequence of the random placement of species ranges within a geographic domain (also known as Périnet effect).

Phenetic biodiversity A characterization of a biota that relates to variation in phenotypic characteristics (traits) of taxa, and is estimated by components that reflect the size of the phenotypic hypervolume defined by constituent taxa, or the dispersion of phenotypes within that hypervolume.

Phylogenetic biodiversity A characterization of a biota that embodies evolutionary history and relates to variation among taxa based on their descent from a common ancestor, often based on the mean and variance of divergence rates or mean and variance of species ages.

Rapoport effect A latitudinal gradient wherein the sizes of the distributional ranges of species decrease with decreasing latitude.

Scale dependence A condition in which either the form or the parameters of a relationship between two variables (e.g., richness and latitude) is contingent on spatial or temporal context.

Species density The number of species per unit of area.

Species diversity A component of taxonomic biodiversity that reflects the variety of organisms in an area and that includes two components, species richness and species evenness (the degree to which all species have the same proportional abundance).

Species richness A component of taxonomic biodiversity that equals the total number of species in an area.

Taxonomic biodiversity A characterization of a biota that relates to variation in the importance, generally measured by proportional abundance, and taxonomic identities of taxa. Metrics that reflect different aspects of taxonomic biodiversity include species richness, evenness, dominance, diversity, and rarity.

Key Points

- The latitudinal gradient of biodiversity (increasing from polar to tropical regions) is essentially a universal pattern that transcends geographic context or taxonomic group.
- The vast majority of research has focused on species richness at broad focal scales; thus, future assessments should consider multiple dimensions of biodiversity (e.g., functional biodiversity, phylogenetic biodiversity) or examine patterns at smaller focal scales, particularly at the community level.
- Considerable controversy and uncertainty remain about the ecological, environmental, evolutionary, or spatial mechanisms that give rise to empirical gradients, but multifactorial explanations are likely to be necessary to account for the gradient.
- Because the Anthropocene is a time of rapid environmental change with respect to global temperatures, the frequency and intensity of climate-induced disturbances, and the extent and magnitude of land use changes, the spatial mapping of salient environmental characteristics will undoubtedly change, with potentially large effects on the nature of future latitudinal gradients.

Latitudinal gradients of biodiversity are biogeographic patterns that define the ways in which components of taxonomic, phylogenetic, functional, genetic, or phenetic biodiversity change with latitudinal position on the surface of the earth. The majority of research has considered only taxonomic biodiversity, and generally has focused on gradients of species richness. Consequently, much of this article summarizes the understanding of latitudinal gradients in species richness. The general pattern is for species richness to increase from polar to tropical regions (Willig *et al.*, 2003; Hillebrand, 2004), regardless of the taxonomic affiliation of organisms (e.g., mammals, fishes, insects, and plants) or geographic setting in which they occur (e.g., Africa, South America, and the Atlantic Ocean). This is true for extant organisms (Fig. 1) as well as for fossilized foraminiferans from the past 70 million years (Fig. 2). An increase in species richness with decreasing latitude is the pattern generally observed at three spatial scales: broad climatic zones (Fig. 3), arbitrary geographic subdivisions (i.e., quadrats or bands) of the earth's surface (Fig. 4), and local ecological communities (Figs. 4 and 5). Nonetheless, the form of the relationship between biodiversity and latitude is not the same for all taxa, and a few groups do not exhibit the general pattern of increasing richness towards the tropics. Moreover, considerable controversy surrounds the mechanisms that affect latitudinal patterns in biodiversity, with ecological, evolutionary, historical, and stochastic processes (Table 1) championed as the principal cause(s) of observed gradients (Rohde, 1992). Indeed, many of the proposed mechanisms are circular or unsubstantiated by empirical data.

Introduction

Since the voyages of Darwin and Wallace, biologists have been fascinated with the high species richness of tropical regions compared to those in temperate or boreal zones. Indeed, this fascination with tropical species richness contributed to the conceptual development of the theories that currently constitute modern ecology. Moreover, increasing concern about the loss of species, especially in tropical regions, has led to the rapid development of the science of conservation biology. Threats to biodiversity arising from climate change have magnified these concerns. Documenting the ways in which biodiversity varies across the globe and understanding the mechanisms that produce such variation are critical steps in the design of global conservation strategies and the implementation of regional management plans.

The mid-1950s to early 1960s saw the emergence of rigorous quantification of broad-scale relationships between species richness and latitude (Fischer, 1960). During the next 25 years, scientists convincingly documented the ubiquity of gradients in which species richness increased toward tropical areas. Similar gradients (Figs. 3 and 4) were quantified for the richness of higher taxonomic groups (e.g., genera, families, and orders). Indeed, the increase in species richness for terrestrial and marine environments was quantified for a wide variety of taxonomic groups, including mammals, birds, reptiles, amphibians, fish, tunicates, crustaceans, mollusks, brachiopods, corals, foraminiferans, and vascular plants. Nonetheless, some taxa (i.e., orders or families) were notable exceptions in having maximal species richness in polar (e.g., seals, penguins, and sandpipers) or temperate zones (e.g., voles, salamanders, ichneumonid wasps, and coniferous trees). Nonetheless, caution must be employed in considering such exceptions because other groups of equivalent rank within the same higher taxon often are restricted to lower latitudes, and the higher taxon exhibits a tropical maximum in species richness.

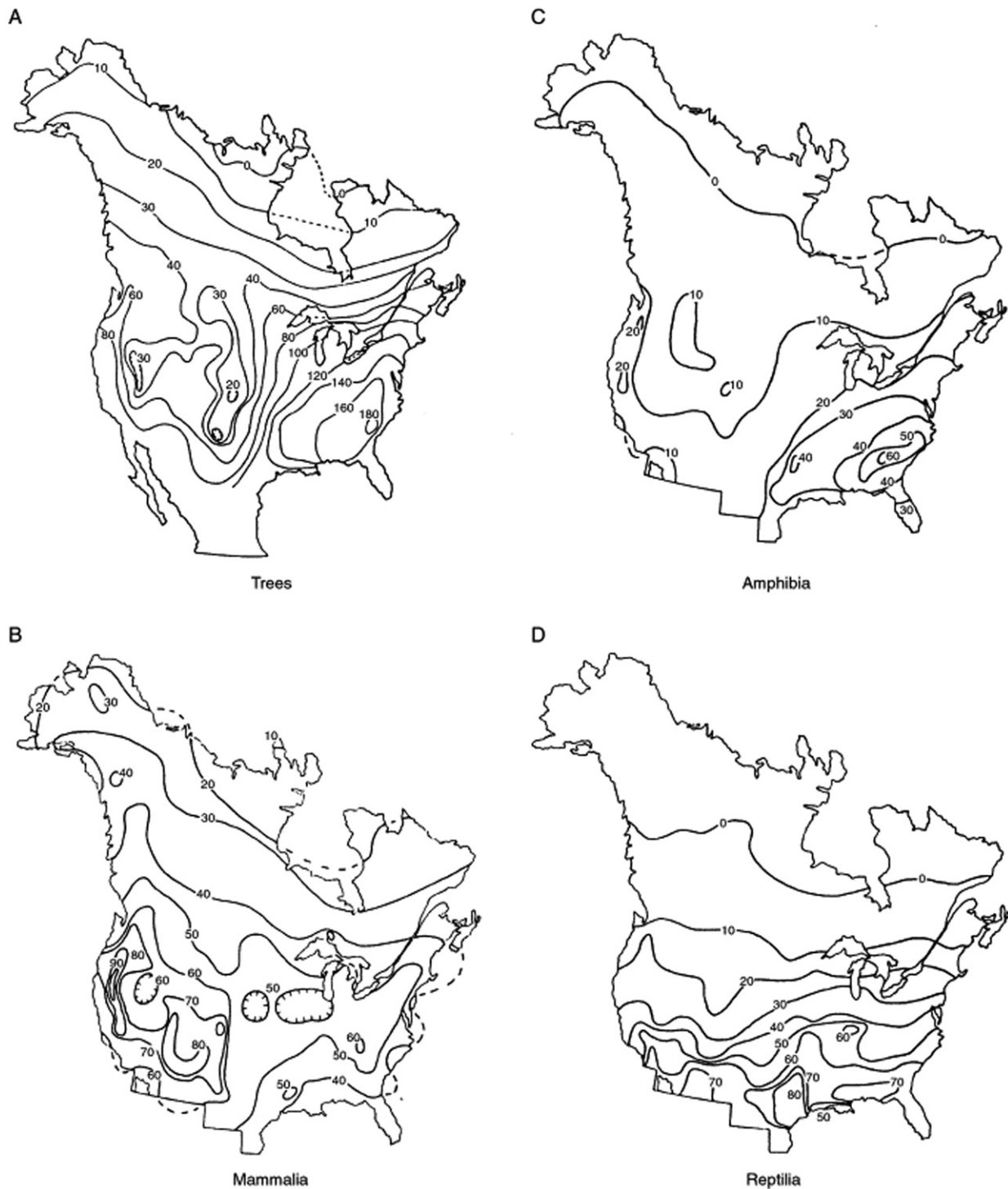


Fig. 1 Species richness gradients in Canada and the United States for trees (A), mammals (B), amphibians (C), and reptiles (D). Contour lines connect localities with approximately equal species richness. Reproduced from Currie, D.J. (1991). Energy and large-scale patterns for animal- and plant-species richness. *American Naturalist* 137, 27–49. With permission from The University of Chicago Press.

Latitudinal gradients in other aspects of taxonomic biodiversity (e.g., evenness, diversity, dominance, and rarity) as well as in other dimensions of biodiversity (e.g., functional, phenetic, genetic, and phylogenetic) have received increasing attention during the past decade. This nascent field of investigation is ripe for exploring the form of gradients, the mechanisms that affect them, and the degree to which they are associated with each other.

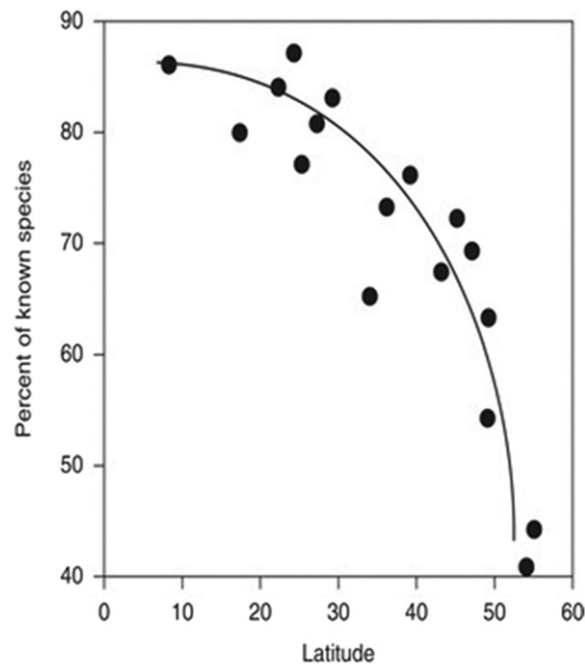


Fig. 2 Latitudinal gradient in fossil species richness for marine Foraminifera from approximately 70 million years ago. Modified from Rosenzweig, M.L. (1995). *Species diversity in space and time*. Cambridge, MA: Cambridge University Press.

Patterns

In the context of this article, a gradient implies a gradual change in biodiversity with a gradual change in latitude. In an unambiguous fashion, the form of that pattern is the precise mathematical or statistical relationship that describes how biodiversity changes with latitude. As a consequence, three considerations are important in assessing patterns: the general shape of the curve (e.g., symmetry, kurtosis, or linearity), the parameters that characterize the relationship, and the degree to which the fit of empirical data to the predicted curve is equivalent to the north and south of the equator. Knowledge of these three aspects of gradients suggests the kinds of causal mechanisms that are in operation. In addition, it facilitates comparison of gradients among taxa within the same geographic domain (Fig. 1; birds, mammals, reptiles, and amphibians in North America) as well as comparisons among different geographic domains for the same taxon (Fig. 4; North America and South America for mammalian orders).

Patterns are often scale dependent, with particular mechanisms having larger effects at some spatial scales than at others. Consequently, patterns can be evaluated at a variety of scales, ranging from biotic assemblages that occupy large areas (e.g., biogeographic regions, biomes, or climatic zones) to ecological communities that occupy local sites. These scales are intimately associated with each other. In part, the species richness of regions, biomes, or climatic zones is a consequence of the species richness that occurs in constituent local communities. Similarly, the species richness and composition of local communities are affected by the set of taxa that constitute regional species pools (Putman, 1994).

Assemblages

Most of the empirical research concerning relationships between biodiversity and latitude considers species richness and has been done using arbitrary sampling units that were based on (1) latitudinal bands, (2) quadrats of fixed area, or (3) quadrats of unequal area defined by lines of longitude (meridians) and latitude (parallels). Alternatively, research has focused on the species richness of biomes or broad latitudinally defined climatic zones. Because the variation in the area of sampling units may have a large effect on variation in species richness, it is critical to understand how area may affect latitudinal patterns in different ways, depending on the method or approach (Scheiner *et al.*, 2000, 2011).

Generally, analyses of quadrats defined by meridians and parallels are inferior to those based on other sampling units because such quadrats differ in area in a systematic fashion and bias conclusions. As meridians converge toward the poles, the size of the quadrats becomes smaller. Consequently, any attempt to control for variation in richness among quadrats as a consequence of area will remove at least some of the effects of latitude as well. This confounding effect compromises the ability to detect patterns across broad latitudinal gradients.

Analyses based on latitudinal bands also must control for the effect of area because the width of a continent is not constant at all latitudes. A variety of methods have been used to compensate for this problem. Importantly, care must be employed when the area of bands varies in a systematic fashion with latitude because of the shape of the continent (e.g., progressive decreases in area

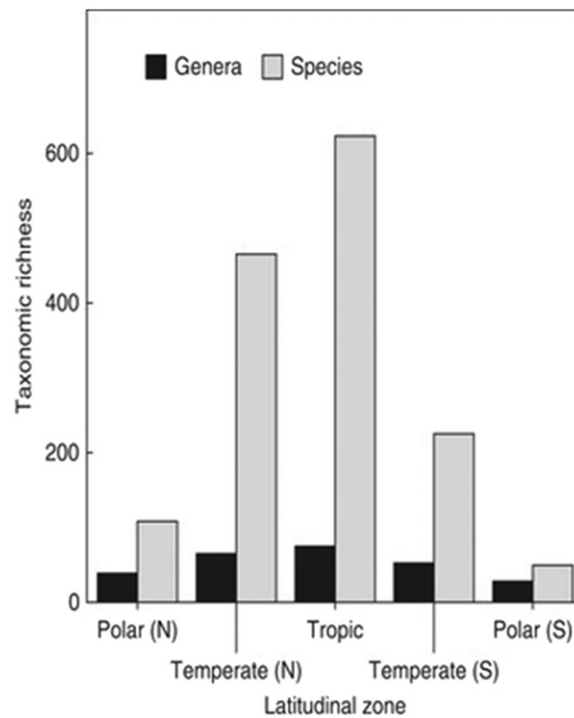


Fig. 3 Generic and species richness of tunicates in each of the five major climatic regions defined by latitude and arranged from northern-most latitudes, through the tropics, to southern-most latitudes. Modified from Fischer, A.G. (1960). Latitudinal variations in organic diversity. *Evolution* 14, 64–81.

with decreasing latitude in North America versus progressive increases in area with decreasing latitude in South America). In such cases, analyses based on bands may be plagued with the same confounding effects as those for analyses based on quadrats defined by meridians and parallels. Indeed, if classical statistical techniques are used to control for the effect of area in bands defined by 5° meridians in North America, the areal relationship is contrary to both common sense and ecological theory in that species richness increases as area decreases. Subsequent assessment of latitudinal effects may be severely compromised because the width of North America decreases as latitude decreases. Hence, adjusting the latitudinal gradient to account for area also removes an appreciable latitudinal effect. Nonetheless, if continental shape does not confound the effects of latitude and area, then regression techniques hold great promise, especially if appropriate nonlinear approaches are used to adjust species richness based on species area theory (i.e., adjust richness of bands to a common area based on nonlinear regression of nested quadrats within each band).

Quadrats of fixed size also have been used to analyze broad-scale patterns of diversity. Nonetheless, variation in species richness among sampling units could still be a consequence of area, at least partially, when quadrats occupy coastal positions along continental borders. Adjusting for area in these cases may obscure the effects of rapid transition zones in terrestrial communities as they approach land–sea margins. Hence, the consensus is to not consider quadrats unless they are full of land. Subsequent variation among quadrats that is due to latitude can be assessed through a variety of statistical models. However, here too it is important to note that patterns are scale dependent (e.g., Lyons and Willig, 2002). That is, the pattern detected for 100 km^2 quadrats could be quite different from those at $10,000 \text{ km}^2$.

Much of the early literature on latitudinal gradients in biodiversity was based on the species richness of broadly defined climatic zones (e.g., north polar, north temperate, tropical, south temperate, and south polar) or geopolitical units (e.g., countries, states, or provinces). Taxonomic richness was documented to increase from polar to tropical regions (Fig. 3). Even when values for richness were not adjusted for the areal extent of geopolitical regions (e.g., snake species in Argentina, ant species in the Americas, and breeding bird species in the Americas), the polar to tropical gradient was obvious. Nonetheless, controversy currently surrounds the interpretation of such data when the focus is on broad climatic zones associated with latitude. Some suggest that the increase in diversity with decreasing latitude primarily is a result of more tropical regions having larger areas than their extratropical counterparts. In contrast, others suggest that extratropical areas are often larger but have fewer species than their more tropical counterparts, implying that latitudinal correlates other than area are the driving forces behind the gradient (see Section “Geographic Area Hypothesis”).

Ecological Communities

The ways in which latitudinal variation in biodiversity at broad spatial scales (i.e., γ -scale) is related to patterns of biodiversity at the level of local communities (i.e., α -scale) is unclear. In part, this is because the geographic boundaries of a community are difficult to designate and are ultimately arbitrary decisions. Moreover, until recently, little was known about the composition of

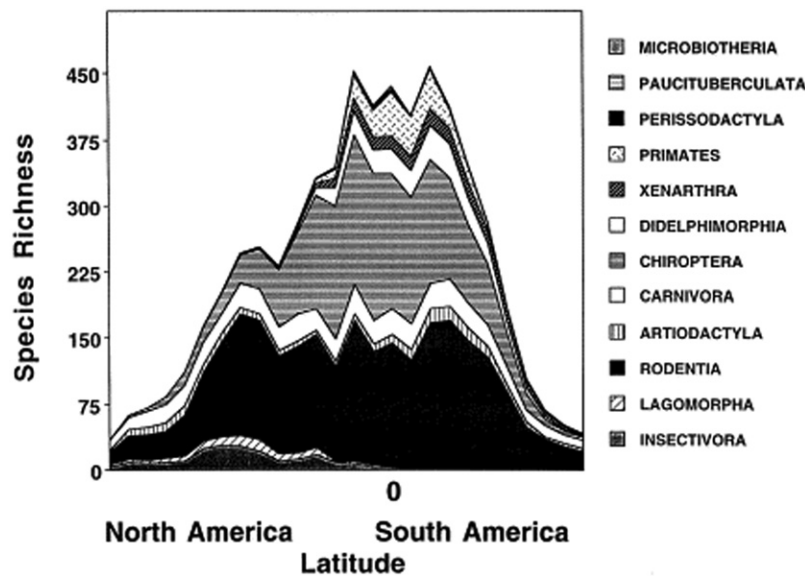


Fig. 4 Differential contribution of mammalian orders to the latitudinal gradient of species richness in the New World based on data from 5° latitudinal bands. Reproduced from Kaufman, D.M. (1995). Diversity of New World mammals: Universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy* 76, 322–334.

local communities in tropical regions, making assessment of broad-scale latitudinal patterns of biodiversity a premature endeavour at the community level. Finally, it is unlikely that a single research scientist can gather sufficient data across many sites to assess latitudinal gradients in biodiversity with sufficient power to distinguish ecological patterns from random variation. Hence, compositional data must be compiled from the work of many different individuals, who often use different methods, designs, and sampling intensities, to quantify the gradient in a meaningful way. Concern regarding adequate sampling within a community (e.g., Voss and Emmons, 1996) must be tempered by the realization that community composition has a temporal dynamic. Communities represent suites of populations with the potential to interact, and thus must be constrained to some extent by both time and space. Sampling regimes that extend over protracted periods of time (e.g., decades or longer) may have inflated estimates of richness and inaccurate assessments of species composition. Nonetheless, recent progress in this regard allows quantitative evaluation of patterns in a rigorous way, at least for some taxonomic groups.

When care is taken so that a local community is delimited as a geographic area in which constituent species have a high likelihood of co-occurrence in space and time, it is clear that species richness increases from polar through temperate to tropical regions. For example, data for bats from 32 local communities (Stevens and Willig, 2002) that met rigorous standards for inclusion in analyses (i.e., well-delimited local areas must have been sampled intensively for at least 1 year to include all seasons in which species are active) clearly exhibit a latitudinal gradient of increasing richness with decreasing latitude (Fig. 5(A)). Species richness of nonvolant mammalian communities from North America also shows a significant increase from polar to tropical regions (Fig. 6; Kaufman, 1998). These community-level patterns may arise because of the negative association of productivity with latitude, which allows communities at low latitudes to support more individuals and enables more species to exceed minimum thresholds for viable populations and to avoid extirpation from stochastic or density-independent events (Stevens and Willig, 2002).

Beyond species richness, taxonomic biodiversity has a number of other interrelated components such as evenness, diversity, dominance, and rarity. Components other than richness arise by weighting the presence of species by some measure of importance such as relative abundance, relative biomass, or relative frequency of occurrence. Moreover, each component can be estimated by indices that differ in the ways in which presence is weighted by importance. Richness is the number of species in a community; it can be equal to the empirical value or can be estimated via extrapolation or rarefaction (Chao *et al.*, 2014). Evenness represents the extent to which the distribution of individuals among species is equable. Diversity is a composite metric, comprising aspects of richness and evenness. Dominance is the extent to which a single taxon represents the largest proportion of individuals in a community. Rarity is a measure of the number of taxa below some threshold level of abundance (e.g., the number of species with less than the average proportional abundance $[1/S]$ in a community of S species). The extent to which each of these components of taxonomic biodiversity exhibits a latitudinal gradient has not been explored for most groups of plants, animals, or microbes. In contrast, the comprehensive analysis of Stevens and Willig (2002) characterized taxonomic biodiversity of New World bat communities based on 14 different indices representing species richness (3 metrics), evenness (4 metrics), dominance (3 metrics), and diversity (4 metrics). They demonstrated that spatial variation in richness was independent of spatial variation in evenness. Moreover, they documented strong latitudinal gradients in species richness and diversity, but the absence of such gradients in species evenness or dominance (Fig. 5).

Many factors (e.g., productivity, competition, predation, and disturbance) have been suggested as the dominant forces affecting the composition and structure of local communities. Early theoretical and empirical work stressed the role of deterministic factors

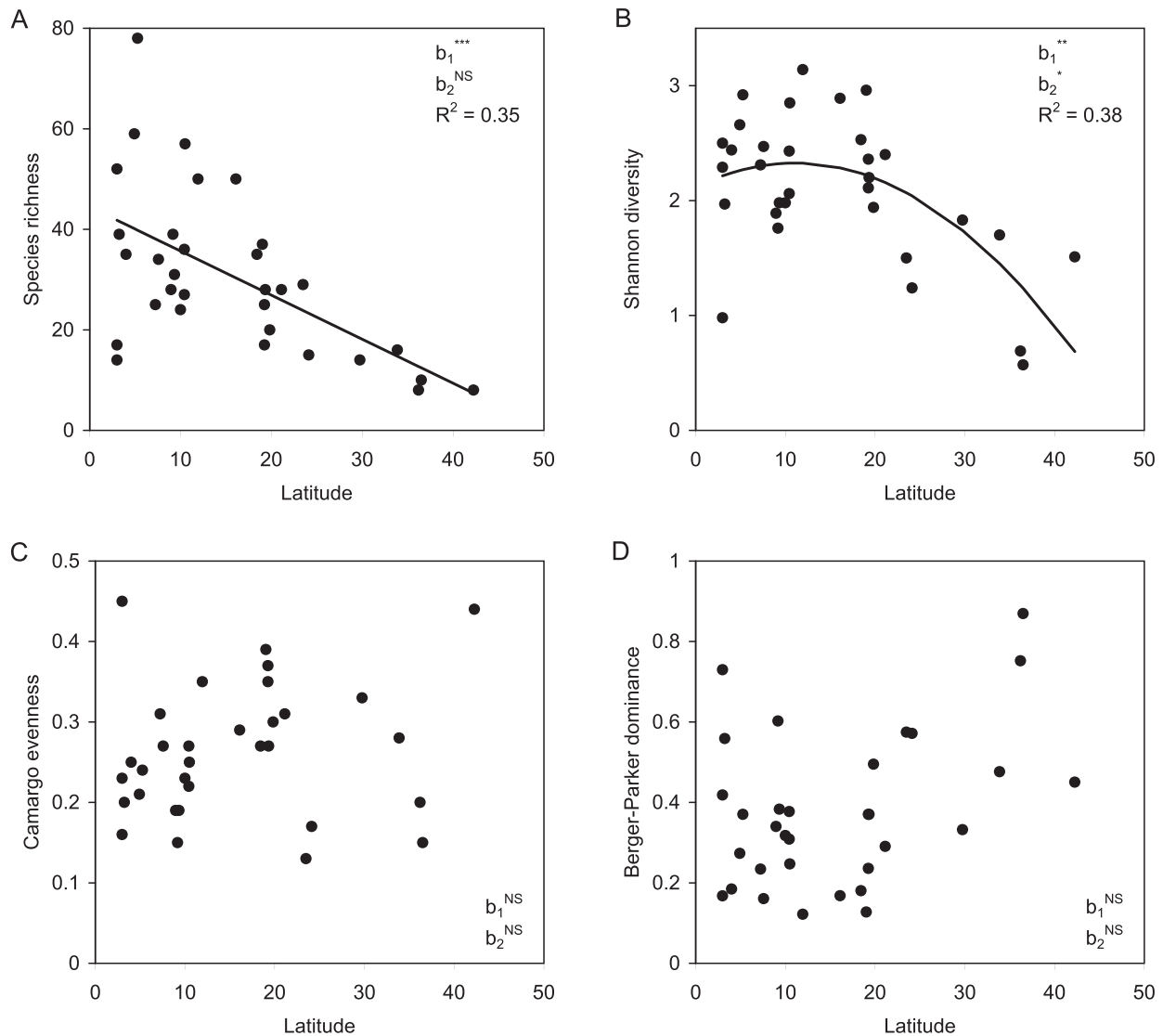


Fig. 5 Latitudinal gradients of the taxonomic dimension of biodiversity – species richness (A), Shannon diversity (B), Camargo evenness (C), and Berger-Parker dominance (D) – within local communities for bats from throughout the New World. When regression models are significant the best-fit line shows the relationship. Contributions of linear (b_1) or quadratic (b_2) terms are indicated by superscripts (NS, $p > 0.05$; *, $0.05 \geq p > 0.01$; **, $0.01 \geq p > 0.001$; ***, $p < 0.001$), and percent variation in a component of taxonomic biodiversity that is related to latitude is quantified by R^2 for significant relationships. Reproduced from Stevens, R.D. and Willig, M.R. (2002). Geographical ecology at the community level: Perspective on the diversity of New World Bats. *Ecology* 83, 545–560.

such as competition in molding community attributes. Subsequent focus on the distinction between equilibrational and non-equibrational communities cast doubt on the universality of deterministic mechanisms in general and competition in particular, and raised serious questions about the degree to which local communities were saturated by species. Indeed, variation in the degree to which local communities attain equilibrational richness may contribute strongly to the latitudinal gradient in biodiversity (Putman, 1994). The latitudinal progression from polar to tropical regions may represent a gradient in the degree to which stochastic density-independent mechanisms or biotic interactions dominate the forces affecting the abundance of local populations and the composition of local communities. Specifically, the species richness of a community may be a consequence of the severity, variability, and predictability of local environmental conditions. Low predictability and harsh conditions predispose communities to be regulated by abiotic parameters and to have low diversity. High predictability and conditions that are clement favour high diversity. To the extent that high solar insolation, warm temperatures, and humid environments represent favorable conditions that increase productivity, and low intra-annual variation in temperature and rainfall represent predictable conditions, tropical communities should be more species rich than their extratropical counterparts. In essence, many of the factors that affect elevated richness at the local scale likely contribute to enhanced γ -diversity of regions as well.

Table 1 Mechanisms potentially affecting the latitudinal gradient in species richness^a

<i>Circular</i>	<i>Empirically unsubstantiated</i>
Competition	Environmental stability
Mutualism	Environmental predictability (contingency)
Predation	Productivity
Epidemics	Abiotic rarefaction
Biotic spatial heterogeneity	Physical heterogeneity
Population size	Angle of the sun above the horizon
Niche width	Area
Population growth rate	Aridity
Patchiness	Seasonality
Epiphyte load	Number of habitats
Host diversity	Rapoport's rule (range size gradient)
Harshness	Ecological time
	Evolutionary time
	Temperature dependence of chemical reactions
	Solar energy
	Evolutionary speed
	Stochastic placement of species ranges

^aModified from Rohde (1992).

Hierarchical Configuration of Biodiversity

The hierarchical configuration of biodiversity is an inherently scale-dependent phenomenon that influences the form and parameterization of latitudinal gradients, as well as the relationship between patterns at local (α) and regional (γ) scales. Indeed, turnover in species composition among local sites contributes to the disparity between biodiversity at local and regional scales, is ostensibly related to habitat heterogeneity, and can be conceptualized via an additive model or a multiplicative model. Unfortunately, considerable confusion and controversy has characterized the discussion of such issues, but a consensus is emerging concerning the meaning and measurement of the β -component of biodiversity in ecological and biogeographic contexts (Tuomisto, 2010), with the multiplicative model rather than the additive model gaining ascendancy, provided that metrics are adjusted to measure "true diversity" (*sensu* Jost, 2007). Moreover, such hierarchical decomposition can be applied to metrics other than species richness, such as species diversity, evenness, dominance, and rarity. In such a context, the β -component of biodiversity is an estimate of the number of taxonomically distinctive communities or compartments along the gradient.

An increase in regional species richness (γ -component) from polar to tropical latitudes can be a consequence of a gradient in species richness at the α -level, β -level, or both. The β -component of species richness increases toward the equator for mammals, birds, shallow water bryozoans, trees, and herbaceous plants (summarized in Willig *et al.*, 2003); however, the exact form of the increase may differ among taxa or between continents. For New World bats, the rate of increase in species richness from extratropical to tropical communities (α -level) is much less than the comparable rate for regional species pools (γ -scale), suggesting that the β -component of richness consistently increases with decreasing latitude (Stevens and Willig, 2002). In contrast, the β -component of richness remained more or less constant below 30° N latitude for nonvolant mammals in North America (Kaufman, 1998). Moreover, the β -component of richness did not contribute to latitudinal gradients of marsupial species richness in North and South America (Willig and Gannon, 1997).

Multiple Dimensions of Biodiversity

The past decade has witnessed increasing interest in understanding how functional, phylogenetic, genetic, or phenetic biodiversity responds to spatial, temporal, or environmental variation, and whether such gradients are any different than those produced by parallel gradients in species richness. Research on latitudinal gradients of multiple dimensions of biodiversity is in its early stages of development, but some of these gradients have been quantified, and shown to have multiple forms that are not wholly explicable by gradients in richness. For ease of exposition, the authors illustrate the state of knowledge for latitudinal gradients of functional, phenetic, and phylogenetic biodiversity based on a comprehensive suite of analyses for 32 communities of New World bats (see Section "Ecological Communities") for which a strong linear increase in species richness accompanies a decrease in latitude (Fig. 7(A)).

The functional dimension of biodiversity can be evaluated based on the consideration of functional traits or on the assignment of species to guilds based on considerations of natural history (e.g., habitat preferences, foraging mode, and diet). Regardless, measures of functional biodiversity evaluate variation in characteristics of a biota that relate to ecosystem processes, species interactions, or functional characteristics of a community. A number of indices of functional biodiversity can be estimated by weighting guilds by some aspect of importance such as relative species richness, abundance (regardless of species), or biomass (regardless of species), giving rise to guild evenness, diversity, or dominance. Nonetheless, the simplest index is guild richness, the empirical number of recognized guilds in a community. Like the latitudinal gradient of species richness, the latitudinal gradient of guild richness of New World bats (Stevens *et al.*, 2003) is strong, and generally increases from extratropical to tropical latitudes; however, the form of the relationship is markedly nonlinear (Fig. 7(B)). Of course, species-rich communities should contain more guilds by chance alone (i.e., selection effects).

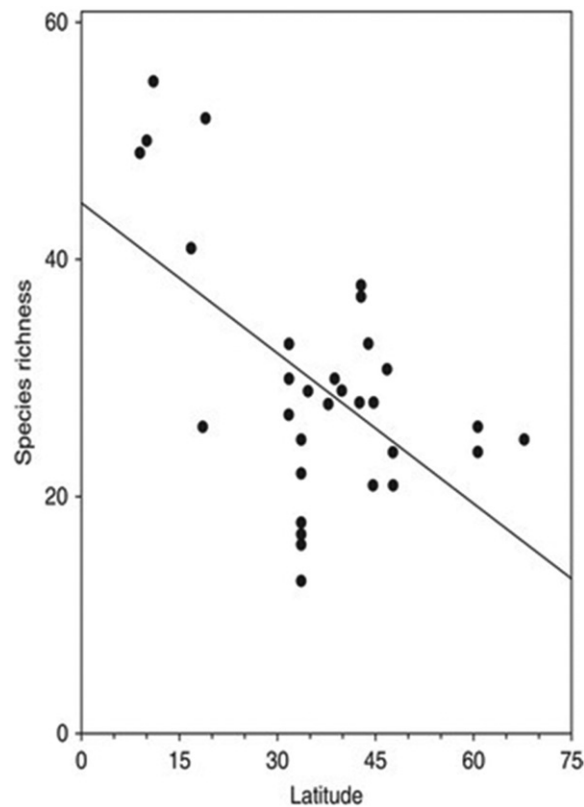


Fig. 6 Latitudinal gradient of species richness for mammalian tetrapods in local communities in North America. Reproduced from Kaufman, D.M. (1998). *The structure of mammalian faunas in the New World: From continents to communities* (Unpublished Ph.D. dissertation). University of New Mexico.

Simulation analyses can evaluate if empirical gradients of guild richness are essentially a consequence of the latitudinal gradient of species richness. Such an approach randomly selects the same number of species that occurs in an empirical community from an appropriate species pool, repeats the random selection process for all empirical communities, estimates parameters of a randomly generated latitudinal gradient in guild richness, and repeats the simulation a sufficient number of times to create a probability density function of parameter values for a gradient created by chance alone. An observed gradient in guild richness is significant if empirical parameter estimates occur in the extreme tails of the generated probability density functions. New World bat communities exhibited a strong and significant latitudinal gradient of guild richness based on such approaches when the suite of bats in the continental New World composed the species pool for each community. In contrast, when each species pool for a community was regional in composition (i.e., a species pool comprised only taxa whose geographic distributions overlapped the site), the empirical latitudinal gradient of guild richness was not different than expected given the observed variation in the composition of regional species pools and the species richness of the community. This indicates that latitudinal gradients in guild richness of communities primarily arise from latitudinal gradients in γ -level richness (i.e., regional species richness). These same approaches were used to assess latitudinal gradients of guild evenness, diversity, and dominance. Guild diversity and dominance significantly, but nonlinearly, increased and decreased toward the tropics, respectively. Like the situation for guild richness, the gradients in guild diversity and dominance were different than those arising from chance alone when considering hemispheric species pools, but not different than expected by chance alone when considering the regional species pool. In contrast, guild evenness evinced random variation with respect to latitude, a pattern expected due to chance, regardless of the nature of the species pool. Taken together, these results suggest that processes, evolutionary or ecological, that determine the composition of regional faunas strongly influence the latitudinal gradient in functional biodiversity.

Phenetic biodiversity reflects variation in phenotypic or morphological characteristics. The ecological attributes of species have a profound association with phenetic characteristics, which can provide an integrated view of ecological relationships over space or time. Different components of phenetic biodiversity relate to aspects of the volume (equivalent to richness) or dispersion (equivalent to evenness) of species within a multidimensional space defined by the phenotypic characteristics of species in a community. If phenetic characteristics relate to foraging mode or diet, such an analysis could be interpreted as a trait-based assessment of functional biodiversity. More generally, the selection of characteristics to be included in analyses determines the kind of phenetic biodiversity that is reflected in resultant components. By measuring a suite of external and cranial characteristics related to the size and foraging apparatus of bats (e.g., skull measurements related to the size and hardness of prey, or wing measurements related to aerodynamic ability), [Stevens *et al.* \(2006\)](#) characterized a number of aspects of phenetic biodiversity. For example, they showed that mean nearest neighbor distances decreased significantly and linearly toward the tropics ([Fig. 7\(C\)](#)), and this trend was different from that expected given the richness of

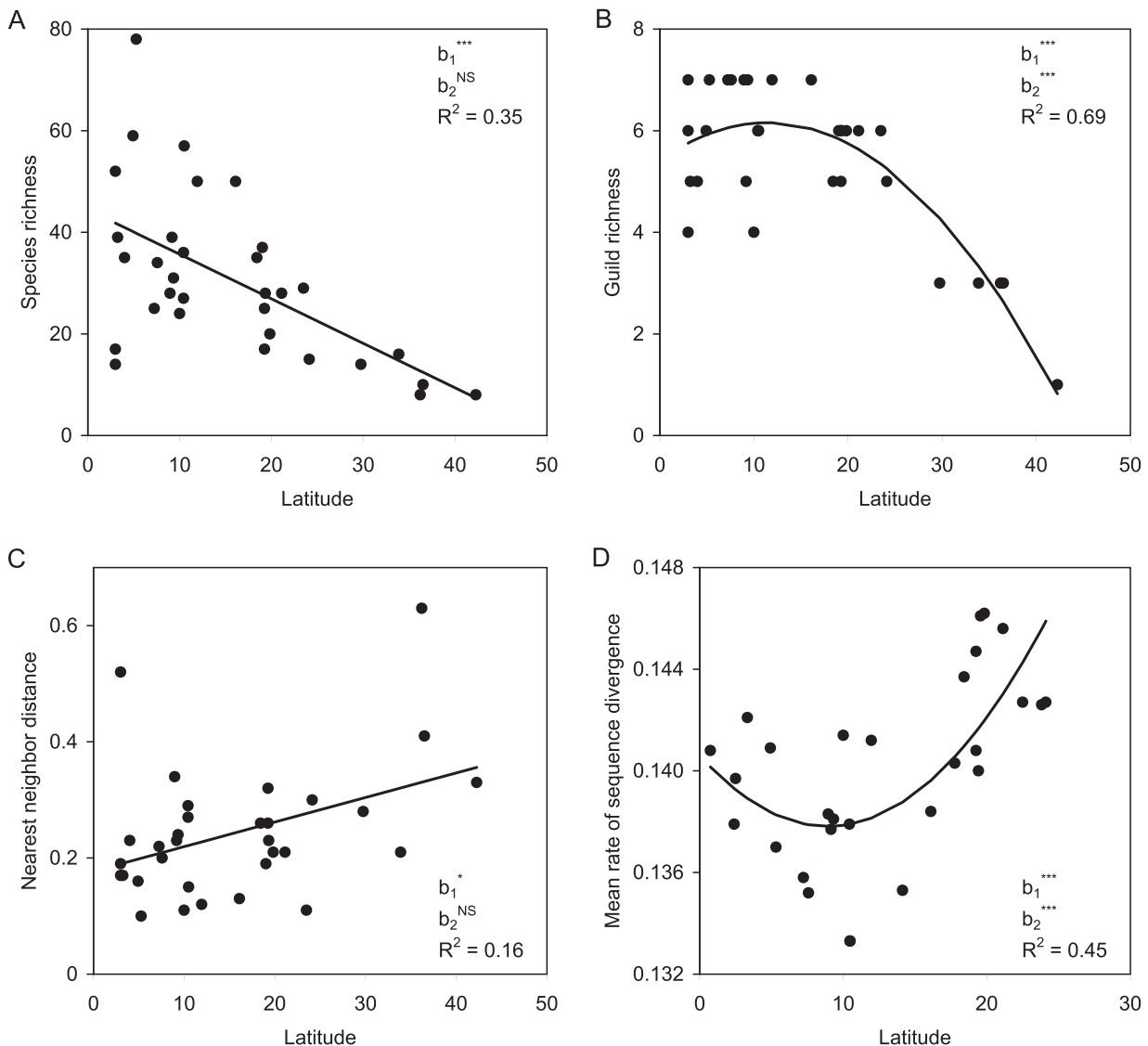


Fig. 7 Latitudinal gradients of taxonomic biodiversity (species richness, A), functional biodiversity (guild richness, B), phenetic biodiversity (nearest neighbor distance, C), and phylogenetic biodiversity (mean rate of sequence divergence, D) within local communities for bats from throughout the New World. Contributions of linear (b_1) or quadratic (b_2) terms are indicated by superscripts (NS, $p > 0.05$; *, $0.05 \geq p > 0.01$; **, $0.01 \geq p > 0.001$; ***, $p < 0.001$), and percent variation in a component of taxonomic biodiversity that is related to latitude is quantified by R^2 . Reproduced from Stevens, R.D. and Willig, M.R. (2002). Geographical ecology at the community level: perspective on the diversity of New World Bats. *Ecology* 83, 545–560. Stevens, R.D., Cox, S.B., Strauss, R.E. and Willig, M.R. (2003). Patterns of functional diversity across an extensive environmental gradient: Vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters* 6, 1099–1108. Stevens, R.D., Willig, M.R. and Strauss, R.E. (2006). Latitudinal gradients in the phenetic diversity of New World bat communities. *Oikos* 112, 41–50. Stevens, R. D. (2006). Historical processes enhance patterns of diversity along latitudinal gradients. *Proceedings of the Royal Society B* 273, 2283–2289.

communities and the composition of the hemispheric species pool, but no different than expected by chance given the richness of communities and the composition of site-specific regional species pools. Again, historical factors affecting regional species pools have a great impact on gradients of phenetic biodiversity.

The phylogenetic dimension of biodiversity reflects the evolutionary history embodied in a community (e.g., the distribution of taxon ages or the magnitude of relatedness within a community). A variety of metrics estimate different aspects of that evolutionary history, and each species contribution to those estimates can be weighted by the aspects of importance (e.g., relative abundance or relative biomass). Stevens (2006) estimated a number of different components of the phylogenetic dimension of biodiversity for New World phyllostomid bat assemblages, and documented gradients based on the average and variance in the rate of sequence divergence, as well as on the average and variance in the relative ages of taxa. For example, the mean rate of sequence divergence in a community decreased from extratropical to tropical latitudes, but did so in a nonlinear manner (Fig. 7(D)). Moreover, the latitudinal gradient in phylogenetic diversity was different from that expected based on the latitudinal gradient in species richness and the composition of the hemispheric species pool. These results

suggest that significant historical events influence contemporary gradients in phylogenetic biodiversity, with the most derived and least variable taxa occurring at the periphery of the geographic range of the family (i.e., in extratropical areas), providing support for the concept of niche conservatism.

Mechanisms

A grand proliferation of hypotheses (Table 1), along with subsequent a posteriori modifications, characterizes the latitudinal gradient literature. Each hypothesis represents a conceptual model with only qualitative predictions. As with much of macroecological research, broad-scale data concerning the distribution of species is not available for many taxa. Manipulative experiments designed to disentangle the effects of competing hypotheses are not feasible or ethical. In addition, the inherent geographic factors that might affect richness are often correlated so that efforts to remove the effect of one to assess the other can lead to spurious results due to the confounded nature of the mechanisms.

Indeed, most of the hypotheses represent conceptual models that lend insight into how nature could operate and provide only a general qualitative prediction that richness should increase toward the tropics, but do not generate unique predictions based on direct features of the gradient that conclusively refute any of the competing hypotheses. Moreover, many hypotheses are circular in nature and the indirect predictions that they make about latitudinal gradients have not been examined comprehensively from an empirical perspective. For example, smaller species ranges, more intense biotic interactions, increased diet specificity, and greater numbers of individuals are all mechanisms that could contribute to latitudinal biodiversity gradients, or conversely, could be consequences of the greater species richness in the tropics. In addition, some hypotheses only pertain to particular taxa or ecological groups, so that they are not applicable universally.

Rather than elucidating the score of extant hypotheses, which has been done to greater or lesser extents elsewhere (Rohde, 1992; Rosenzweig, 1995; Gaston, 1996), an exposition of selected hypotheses that have generated considerable debate in the literature follows.

Geographic Area Hypothesis

The latitudinal gradient in which richness peaks in the tropics may be a consequence of the larger landmass of the tropics compared to other geographic zones. This simple idea had its genesis in the work of Terborgh (1973), with considerable development and refinement by Rosenzweig (1995), who incorporated the effects of productivity and zonal bleeding into a more comprehensive conceptual model. Nonetheless, the geographic area hypothesis has generated considerable controversy and contention (Rohde, 1997, 1998; Rosenzweig and Sandlin, 1997). The controversy does not surround whether an areal mechanism operates; rather, it focuses on the degree to which variation in area is the dominant factor molding latitudinal gradients in richness. Importantly, any hypothesis about effects of area on biodiversity is driven by ecological processes. The primary bases for effects of area on biodiversity are related to increased productivity, environmental variation, and the number of individuals that can be supported by larger areas. Even hypotheses about the effects of diversification rates (see next section) on biodiversity rely on relationships between abundance and the likelihood of extinction, speciation, and mutation. Consequently, even evolutionary and geographical hypotheses often have local ecological mechanisms as part of the conceptual bases for their predictions.

Two features of the earth's geometry predispose the sizes of tropical regions to be greater than those of their higher latitude counterparts. First, the earth is essentially a sphere. The distance between longitudinal meridians at the equator is greater than that elsewhere on the globe, and inter-meridian distance decreases in a regular fashion toward the poles. Second, northern and southern tropical zones are adjacent, whereas the northern and southern variants of other latitudinally defined zones are isolated from each other. Nonetheless, the positions, sizes, and configurations of the earth's continents will affect the proportion of land or water at each latitude, and this has varied over geological time as a consequence of plate tectonics. In addition, the number and breadth of zones used to subdivide latitude will affect the perception of areal dominance associated with the tropics. For example, a tripartite division (tropical, temperate, and polar) of terrestrial environments reveals that the tropics rank second in area to northern temperate regions at the global scale, with considerable variation in the proportional area represented by the tropics among continents (approximately 38%, 12%, 80%, 41%, and 0% of America, Eurasia, Africa, Australia, and Antarctica, respectively). In contrast, finer resolution of terrestrial zones to tropical, subtropical, temperate, boreal, and tundra indicates the areal predominance of tropical lands globally.

Most important, the degree of environmental variation within the tropics is less than that in other geographic zones, at least with respect to incident solar radiation and temperature. Specifically, a band of 50° centered on the equator evinces no or little change in mean annual temperature with latitude (constant at approximately 27°C), whereas mean annual temperature decreases thereafter by approximately 0.75°C per degree latitude. Hence, regardless of the size of zonal subdivisions chosen to define tropical or extratropical regions, tropical landmasses are larger than any other landmasses with similar variation in temperature.

As a consequence of the areal extent and homogeneity of temperature and solar insolation in the tropics, speciation rates there should be higher and extinction rates lower than in extratropical regions. Specifically, the larger area of the tropics allows its species to have larger ranges than do their extratropical counterparts. Larger ranges allow species to be represented by more populations or populations of larger size, both diminishing the likelihood of extinction and enhancing the likelihood of rescue effects. In addition, tropical areas are more productive than their extra-tropical counterparts and support more individuals, which reduces the likelihood of stochastic extinction and

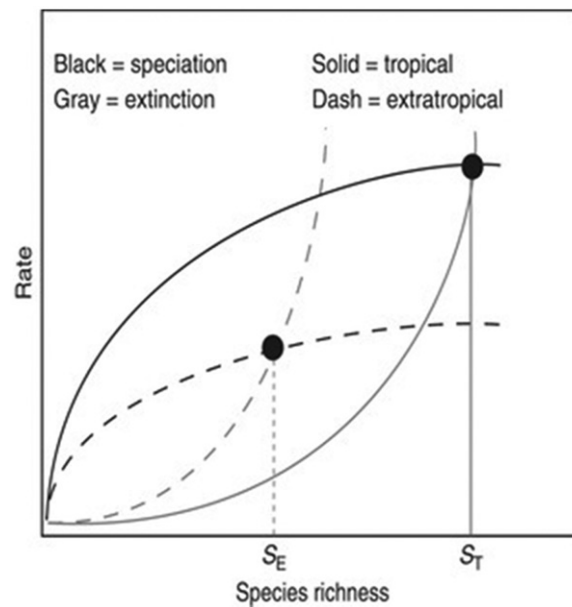


Fig. 8 Graphical model illustrating the dynamic equilibrium between rates of speciation and extinction for tropical and extratropical latitudes. Modified from Rosenzweig, M.L. (1995). *Species diversity in space and time*. Cambridge University Press, Cambridge, MA.

increases the likelihood of speciation, thereby enhancing species richness. Simultaneously, larger areas are more likely to contain or experience events that produce geographic barriers that enhance the rate of allopatric speciation. The dynamic balance between the rates of speciation and extinction, therefore, yield higher equilibrium richness in the tropics than in extratropical areas (Fig. 8).

Rosenzweig and colleagues marshal many lines of evidence in support of the geographic area hypothesis by citing two kinds of observations. First, larger biotic provinces, regardless of latitude, have more taxa than do their smaller counterparts (e.g., generic, familial, and ordinal richness of mammals increase with provincial area). Second, diversities from the same biome but from different continents or provinces differ as a function of their areal extent (e.g., rain forest vertebrates and plants as well as tropical freshwater fish increase in richness as their areal extent increases). Situations in which the general pattern does not occur usually include large but unproductive climatic zones with few species – effectively the richness-diminishing effects of low productivity may countermand the dominant role of area in these systems. An analysis of vertebrate species richness in 32 biotic provinces supports the importance of area as a contributor to latitudinal richness gradients, contemporary patterns of species richness are best explained by a model that includes historical area and productivity through geological time (Jetz and Fine, 2012). Importantly, the combination of historical area and productivity likely are underlying causes of spatial variation in rates of speciation, extinction, and diversification (see next section). In contrast, Rohde (1997) considers area not to be the dominant factor that affects high species richness in the tropics. He illustrates the point with Eurasian freshwater fishes, and shows that much smaller tropical regions have much greater species richness than do larger cold-temperate regions. Similarly, the expansive deep-sea biome with more or less constant temperature has far fewer species than its smaller tropical counterparts. Although a consensus regarding the relative importance of area in shaping latitudinal gradients of richness remains elusive, currently available data suggests that effects of area on latitudinal richness gradients may differ between terrestrial and aquatic biomes.

Because bats exhibit exceptionally strong latitudinal gradients of richness at multiple spatial scales in the New World, they are a useful fauna with which to test the geographic area hypothesis (Willig and Bloch, 2006). Importantly, current ecogeographic zones of the New World (biome types and their constituent biogeographic provinces, *sensu* Udvardy, 1975) are not larger at tropical versus extratropical latitudes, and the spillover of tropical species into ecogeographic zones within extratropical 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 for all bats, as well as for the three most species-rich families (Molossidae, Phyllostomidae, and Vespertilionidae). 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 driver of the pattern.

Speciation, Extinction, and Diversification Rates

After a broad and incisive review of the various mechanisms purported to cause latitudinal gradients in species richness, Rohde (1992) found them all to be lacking. Instead, he suggested that the gradient was a consequence of differential rates of speciation associated with an important latitudinal correlate, temperature, rather than being a product of equilibrium-based ecological processes that presupposed that local communities are saturated with species. His conceptual model is erected on the foundation of three premises. First, tropical environments support shorter generation times for many homeotherms and poikilotherms. Second, mutation rates increase as temperature increases and are highest in the tropics. Third, physiological processes occur faster

at higher temperatures; this, coupled with the first two relationships, suggests an accelerated rate of fixation of favorable alleles in tropical populations. This effectively results in greater evolutionary time in the tropics for mechanisms of diversification to attain fruition. More recently, speciation rate has been combined with extinction rates into a single hypothesis: the diversification rate hypothesis, which posits that speciation rates will be greater and that extinction rates will be lower in the tropics. In concert, these mechanisms result in greater diversification rates (i.e., speciation rate minus extinction rate) in the tropics and result in the tropics being both a “cradle” and a “museum” of diversity (Chown and Gaston, 2000; Fine, 2015).

The potential effect of diversification rates on latitudinal gradients of species richness has been evaluated for terrestrial and aquatic ecosystems as well as for vertebrate and invertebrate taxa. Many studies found support for increased diversification rates contributing to latitudinal gradients of species richness; however, support for diversification rates as important drivers of latitudinal diversity gradients is taxon specific. For planktonic foraminiferans, temperature affects per individual speciation rates, contributing to the latitudinal gradient of species richness (Escarguel *et al.*, 2008). Similarly, diversification rates of swallowtail butterflies increase with temperature (Condamine *et al.*, 2012). In addition, gradients of swallowtail species richness have closely tracked changes in temperature through evolutionary time regardless of latitude. In contrast, there was no relationship (direct or indirect) between latitude and speciation rates in birds (Bromham and Cardillo, 2003). Rather than particular environmental conditions, rapid shifts between climatic regimes cause greater species richness for birds in the tropics (Kozak and Wiens, 2010), with sister species being more climatically divergent in the tropics and niche conservatism being the rule in temperate zones (Kozak and Wiens, 2007). In addition, the richness gradient for basal bird taxa is indistinguishable from that for all birds, whereas the richness gradient for derived taxa is much shallower (Hawkins *et al.*, 2006).

Understanding the effects of diversification rates is also not straight forward for analyses of the evolutionary history of mammals. Speciation and extinction rates for the entire mammalian phylogeny have been greater in the tropics than in the temperate zone (Rolland *et al.*, 2014). In addition, analyses restricted to particular mammalian orders found greater speciation rates, lower extinction rates, or both for primates, lagomorphs, Australasian marsupials, ungulates, shrews, bats, and rodents. In contrast, comparisons of diversification rates between tropical and temperate genera of mammals failed to detect latitudinal differences in speciation or extinction rates (Soria-Carraco and Castresana, 2012). These apparently contrasting results indicate that contributions of diversification rates to the latitudinal diversity gradient occurred early in the history of mammals (Rolland *et al.*, 2014). In general, there is no positive relationship between temperature and species richness of mammalian clades (Buckley *et al.*, 2010). Rather, environmental niches of clades are phylogenetically conserved, and clades differ in their climatic origins (i.e., clades of tropical origin may have positive temperature-richness relationships, but clades of temperate origin tend to have negative temperature-richness).

With the recent proliferation of highly resolved phylogenies, a meta-analysis of 111 phylogenies from mammals, birds, insects, and flowering plants was conducted to evaluate support for various evolutionary hypotheses associated with the latitudinal gradient in biodiversity (Jansson *et al.*, 2013). In addition to the diversification rate hypothesis, the study evaluated the support for the “out-of-the-tropics” hypothesis (Jablonski *et al.*, 2006), which postulates that lineages originate in the tropics, diversify, and then disperse into temperate regions as well as the “tropical niche conservatism” hypothesis (Olalla-Tárraga *et al.*, 2011), which suggests that lineages that originate in the tropics have difficulty adapting to extra-tropical climates, resulting in an accumulation of taxa restricted to tropical environs. Results supported the out-of-the-tropics hypothesis, with an interesting new aspect: lineages that remained in the tropics diversified more quickly than did sister lineages that dispersed to higher latitudes, indicating that diversification rates may be tied to niche conservatism. In concert, these results suggest that climatic dynamics through evolutionary time and effective evolutionary time, rather than evolutionary speed per se, may contribute to latitudinal gradients of species richness (Fine, 2015).

Rapoport-Rescue Hypothesis

As its name implies, this hypothesis is a hybrid of two mechanisms operating in tandem: the Rapoport effect and the rescue effect. A geographic pattern in which species range size decreases from high to low latitudes came to the forefront of the macroecological literature a few decades ago (Stevens, 1989, 1992), and has been termed Rapoport’s rule after the Argentinian scientist who first discussed the pattern in the context of areographic principles. Stevens hypothesized that the latitudinal propensity for range size to decrease toward the tropics, when combined with differential movement of individuals from source to sink habitats (rescue or mass effects), can generate the latitudinal gradient of diversity.

Specifically, at any one locale in the temperate zone, an individual must be able to tolerate considerable intra-annual variation in climatic conditions; thus, species that occur in the temperate zone can attain a wide latitudinal distribution because of the broad tolerance of its constituent individuals to varying local conditions. In contrast, an individual in the tropics experiences little seasonal variation in climatic conditions; consequently, species comprising individuals that occur in tropical zones are predisposed to have narrower latitudinal distributions. This creates the Rapoport effect. Because little variation in climate characterizes a 50° band centered on the equator, tropical species can have potentially large ranges without adapting to a range of climatic conditions. To span a similar latitudinal area, extra tropical species, on average, would have to adapt to a temperature range of 37.5°C, spanning latitudes from the subtropics into the Arctic Circle (e.g., from 25° to 75°). Although seasonality may affect richness, it is unclear how it would restrict the range sizes of tropical species.

The rescue effect is a phenomenon whereby local extinction of a population, often in marginal or sink habitats, is prevented because of immigration of individuals from high-quality or source habitats. Because smaller ranges, which are differentially situated in the tropics as a consequence of the Rapoport effect, have greater perimeter to area ratios, they are predisposed to having greater rescue effect areas relative to range areas. This would differentially inflate species richness in tropical areas and generate latitudinal gradients of diversity.

The generality of Rapoport's rule, as well as the degree to which empirical patterns are generated by the hybrid mechanisms embodied in rescue and Rapoport effects, are controversial. The Rapoport effect has been documented for a diversity of taxa (mammals, reptiles, amphibians, fish, crayfish, amphipods, mollusks, and trees) in aquatic and terrestrial environments, and quickly became engrained as the explanation for species diversity gradients in a variety of ecology textbooks. Additional circumstantial evidence was derived from the observation that taxa that do not show the general latitudinal gradient in richness also do not adhere to Rapoport's rule, suggesting that both patterns had a shared mechanistic basis (Stevens, 1989). Nonetheless, a growing body of evidence suggests that the Rapoport pattern is far from universal (Rohde *et al.*, 1993; Lyons and Willig, 1997). Moreover, reanalysis of data on marine mollusks that was used to corroborate the Rapoport effect (Stevens, 1989) failed to produce the same patterns in a subsequent study, even though the methods were the same in both studies (Roy *et al.*, 1994). In addition, New World bats and marsupials (Lyons and Willig, 1997; Willig and Lyons, 1998), as well as nonmigratory marine teleosts from surface waters (Rohde *et al.*, 1993), each exhibit strong latitudinal gradients in diversity but do not adhere to Rapoport's rule. Hence, occurrences of latitudinal gradients in diversity do not have one-to-one correspondence with the existence of a Rapoport effect.

Simulation models provide added insight into the phenomenon of Rapoport's rule. The three commonly used methods (i.e., Stevens', midpoint, and most distal point) for assessing a Rapoport effect suffer from serious limitations. Stevens' method is problematic because of a lack of independence associated with counting the same species multiple times in the same analysis (Rohde *et al.*, 1993). Midpoint and most distal point methods suffer from severe mathematical biases – the bounded nature of continents or oceans predisposes correlations between range size and latitude even when ranges are distributed stochastically with respect to latitude (Colwell and Hurtt, 1994; Lyons and Willig, 1997). Finally, a comprehensive set of simulation models (Taylor and Games, 1999) suggests that the Rapoport effect causes a latitudinal pattern in species richness, but the gradient is opposite of the pervasive pattern found in nature, in that species richness increases with increasing latitude. Moreover, incorporation of a rescue effect into the model so that it reflects the Rapoport–rescue mechanism fails to rescue the hypothesis; the predicted pattern remains a decrease in richness toward the tropics. Only the incorporation of competitive effects either to the simulation model based on the Rapoport effect alone or to the combined Rapoport–rescue mechanism produces latitudinal gradients that are consistent with real-world patterns, and in both scenarios, communities must be saturated at equilibrium compositions.

Geometric Constraints Hypothesis

One of the newer ideas to explain latitudinal gradients in biodiversity is the geometric constraints hypothesis (Colwell and Hurtt, 1994; Willig and Lyons, 1998). Geographic constraints may affect patterns of species distribution within a domain, creating modal patterns of biodiversity in the middle of the domain (i.e., the mid-domain effect; Colwell and Lees, 2000). Within the context of latitudinal gradients, this hypothesis would consider peak biodiversity in the tropics to be a consequence of the bounded nature of terrestrial and aquatic habitats. Indeed, both simulation (Colwell and Hurtt, 1994; Pineda and Caswell, 1998) and analytical (Willig and Lyons, 1998; Lees *et al.*, 1999) null models suggest that species richness of a biota should increase toward the center of a shared geographic domain in a quasiparabolic or parabolic fashion as a consequence of the random placement of species ranges within the domain. Other mechanisms proposed to account for latitudinal gradients only suggest qualitative increases in richness with decreasing latitude. In contrast, geometric constraint models make quantitative predictions concerning the form of the latitudinal gradient so that expected values for richness occur for each latitude and can be compared to empirical data.

Multiple null models that differ in the number and type of constraints have been developed to evaluate this geometric hypothesis. The fully neutral model (Colwell and Hurtt, 1994; Willig and Lyons, 1998) defines the expected pattern of species richness while ignoring potential effects of extant environmental gradients, as well as the history of the domain, on range sizes of species. Other null models apply additional constraints on randomizations, such as requiring the range size frequency distribution (RSFD) or the distribution of midpoints in the domain to equal the empirical distribution. For the fully neutral model, the number of species at any point within the domain (S_p) is related only to the proportional distance of that point from the boundary (p) and the number of species in the species pool (S), and is given by $S_p = 2p(1 - p)S$. This model (Fig. 9) is an incarnation of both the two-hit broken stick model and the binomial distribution. In essence, if the latitudinal domain of a biota is rescaled to range from 0 in the south to 1 in the north, then the likelihood of a species range overlapping any point P that is exactly p from the southern terminus (and hence $1 - p$ from the northern terminus) of the domain is:

$\Pr(P) = 1 - p^2 - (1 - p)^2 = 2p - 2p^2$, where p^2 is the proportion of species whose northern and southern boundaries lie to the south of P , and $(1 - p)^2$ is the proportion of species whose northern and southern boundaries lie to the north of P . The functional form of the distribution of $\Pr(P) = 2p - 2p^2$ is a parabola that peaks at 0.5, and as a consequence, the average range size of species in the biota is half the extent of the domain (0.5).

Distributions of range midpoints and RSFDs are the collective product of responses to environmental gradients, biotic interactions, and historical processes (Hawkins *et al.*, 2005). Consequently, null models that use such constraints incorporate empirical responses to environmental variation and historical processes into “null” patterns that are produced by the randomization. Constrained models produce a quasiparabolic curve that becomes increasingly flattened as mean range size diverges from 0.5 (the mean value in the fully neutral model). If the mean range size is > 0.5 , species richness in the middle of the domain will be higher and the peak broader than that for a comparable fully neutral model. Alternatively, a RSFD with a mean range size < 0.5 will have a richness peak that is lower and broader than that of a RSFD with a mean range size of 0.5 (Colwell *et al.*, 2004).

Considerable debate exists about the application, utility, and interpretation of geometric constraint null models with respect to empirical data (e.g., Colwell *et al.*, 2004, 2005; Zapata *et al.*, 2003, 2005; Hawkins *et al.*, 2005). Importantly, these null models provide



Fig. 9 Graphical representation (parabola) of the gradient of species richness that arises from the random placement of species ranges within the latitudinal bounds of the New World, scaled from 0 in the south to 1 in the north. The number of species at any latitude is determined by its proportional distance (p) from the southern boundary and is given by $(2p - 2p^2)S$. The vertical lines labeled A and B represent the latitudinal extents of bats and marsupials, respectively. Modified from Willig, M.R. and Lyons, S.K. (1998). An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos* 81, 93–98.

baseline expectations for gradients of species richness in domains in the absence of ecological and evolutionary mechanisms, for the fully neutral model, or given particular distributions of midpoints or species range sizes, for models that incorporate additional biological constraints. Consequently, deviations from null model predictions should be the focus of interpretation for empirical applications of geometric constraint models. For example, a geometrically constrained null model was able to account for 69%–95% of the latitudinal variation in species richness for New World bats and marsupials (Fig. 10; Willig and Lyons, 1998), indicating that latitudinal richness gradients for these taxa approximate null expectations for models that incorporate empirical RSFD, and the ecological and evolutionary mechanisms they represent. Nonetheless, systematic deviations from the null distribution were observed for each taxon, and these deviations represent important foci for further inquiry into mechanisms that mold latitudinal gradients of biodiversity.

Geometric constraint models make predictions (i.e., estimates based on null models) for multiple aspects of latitudinal richness gradients, including the precise shape of the symmetrical curve, as well as the size and location of the single peak in species richness. A comprehensive analysis of geometric constraints on gradients associated with latitude, longitude, ocean depth, or elevation found poor congruence between empirical patterns and those generated by geometric constraint models (Zapata *et al.*, 2003). Nonetheless, this exercise is valuable as systematic deviations from null model predictions can generate more specific hypotheses about mechanisms that shape gradients of species richness. In addition to one-dimensional models, two-dimensional models based on latitudinal and longitudinal constraints have been used to more fully evaluate the potential for geographic constraints to mold gradients of richness. Two-dimensional models fit empirical data more poorly than do one-dimensional models associated with latitude (Zapata *et al.*, 2003; Kerr *et al.*, 2006). Geometric constraints provide the greatest insights when the axis of constraint that defines the domain is associated with important environmental gradients (e.g., latitude, elevation, and ocean depth), such that deviations from predictions suggest possible causal mechanisms.

A geometric constraint approach can enhance the understanding about the relative contributions of evolutionary, environmental, and historical factors to latitudinal gradients of biodiversity. Because, random processes may predispose particular biotas to produce gradients with peaks in richness at tropical latitudes, the challenge for large-scale ecology is to understand the mechanisms that result in deviations from such null models, create peaks in biodiversity, and define the form of the latitudinal gradient in biodiversity.

Assessment and Synthesis

The development of theory can be viewed from a variety of perspectives that deal with the detection of patterns, the association of patterns to processes and mechanisms, and ultimately the integration of those constructs to other theories in the discipline (Pickett *et al.*, 1994; Scheiner and Willig, 2011). The theory of latitudinal gradients of biodiversity has matured considerably during the past 30 years. The

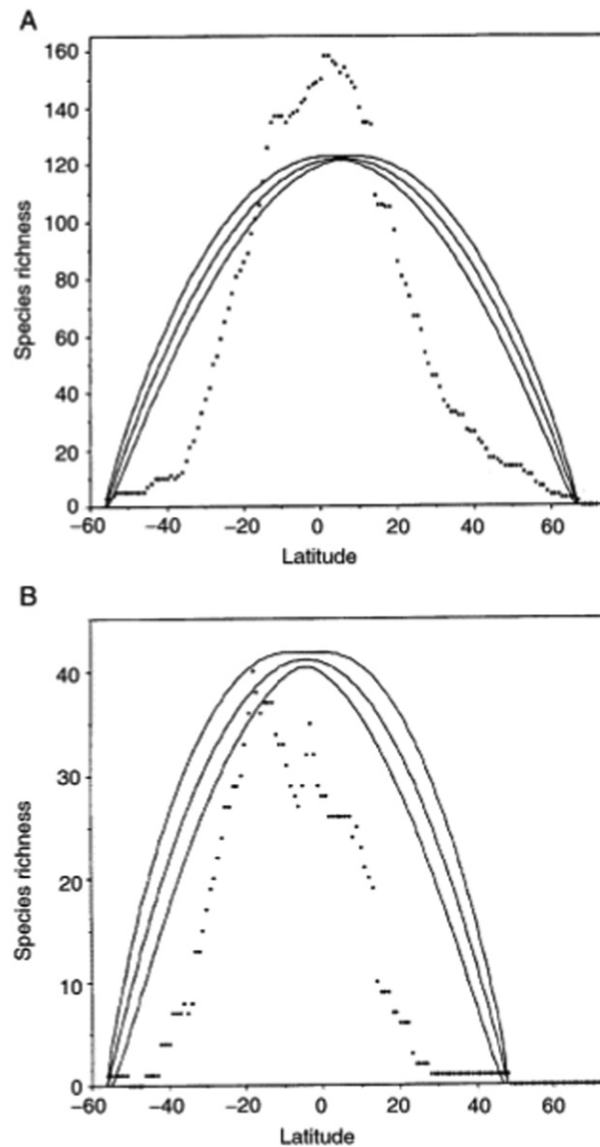


Fig. 10 Comparison of the empirical latitudinal gradient of species richness (dots) with the predicted values (outer lines represent 95% confidence bands, and inner lines represent predicted values) generated by a null model constrained only by the distributional bounds of the fauna for bats (A) and marsupials (B) in the New World. Modified from Willig, M.R. and Lyons, S.K. (1998). An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos* 81, 93–98.

general patterns of latitudinal increase in species richness remain well documented from an empirical perspective. Meta-analyses on more than 500 published latitudinal gradients (Hillebrand, 2004) reaffirmed the generality of the established pattern based on considerations of effect sizes (slopes and coefficients of determination). This analysis established that patterns were stronger and steeper for regional biotas than for local communities, but that the latitudinal extent of the domain did not affect the nature of the gradient. The relationships in marine and terrestrial environs were stronger and steeper than those in freshwater environs, and the gradients were different among continents but not between northern and southern hemispheres. Body mass, trophic level, and thermoregulatory capacity of the targeted biota also affects the strength and shape of latitudinal gradients of biodiversity.

The manner in which particular mechanisms could affect patterns of species richness has become clearer, and elements of the theory have been used to understand other gradients of biodiversity, such as those related to elevation, depth, or productivity. Moreover, latitudinal patterns of species richness are being integrated with other broad-scale patterns concerning the dominance and turnover of species, as well as to latitudinal patterns of range size and abundance, representing a significant advancement in understanding and integration. The past decade has seen renewed interest in evolutionary and historical mechanisms in addition to those of a more ecological nature.

Although few of the hypotheses postulated to affect the latitudinal gradient in species richness have been eliminated in a conclusive manner, research concerning many of the mechanisms appears more likely to advance theory in the near future. Indeed, recent synthetic works have focused on them to a great extent. Understanding the contexts and degrees to which area, climatic

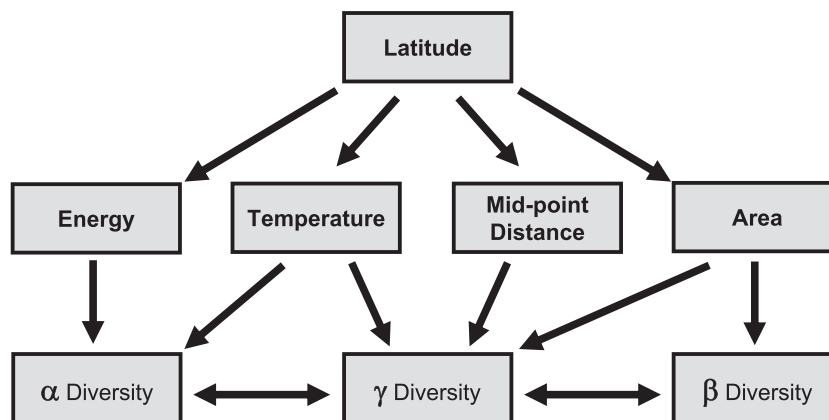


Fig. 11 Conceptual model indicating likely mechanisms whereby latitude may affect α -, β -, or γ -diversity. Latitude is a surrogate for correlated spatial or environmental characteristics (e.g., energy, temperature, area) with which it covaries. These spatial and environmental covariates figure centrally in dominant hypotheses associated with the latitudinal gradient in species richness. Modified from Willig, M.R., Kaufman, D.M. and Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics* 34, 273–309.

variability or stress, geographic constraints, productivity, temperature, and their interactions mold the latitudinal gradient in diversity remains a challenge for scientists to synthetically address in the coming decade. For example, the synthesis by Willig *et al.* (2003) provides a conceptual model (Fig. 11) of how latitude as a surrogate for considerations of energy, temperature, geometric constraints, and area (hypothetical mechanisms for the latitudinal gradient) differentially affects species richness at different focal scales as well as the association between them.

In contrast to the situation regarding species richness, the state of theory regarding latitudinal gradients of other aspects of the taxonomic dimension (e.g., evenness, diversity, and dominance) or of other dimensions of biodiversity (e.g., functional and phylogenetic) is in its early stages of development. General latitudinal patterns for aspects of biodiversity other than species richness have not been well established. Moreover, the mechanistic bases of these more complex gradients have been explored only in a rudimentary manner. Nonetheless, it is clear in the limited number of cases where they have been explored that latitudinal gradients in other dimensions of biodiversity are not wholly explicable by gradients in species richness and that historical factors likely play an important role in shaping these gradients.

Concluding Remarks: Gradients in the Anthropocene

Drivers of global change (i.e., warming, increased frequencies of extreme events [e.g., droughts, floods, wild fires, hurricanes], and land use change) will continue to alter the mapping of environmental attributes onto geographic space, sometimes creating novel environments without contemporary analogs (e.g., Urban *et al.*, 2012). Depending on the rate and magnitude of environmental change, species composition and richness will change in local communities or at latitudes as a result of combinations of local or regional extinction and immigration and emigration dynamics in response to shifting environments. Over evolutionary time, new latitudinal patterns may emerge depending on the correspondence between rates of origination and rates of environmental change (e.g., species may not be able to adapt to rapidly occurring local change or may be unable to effectively track geographic locations with hospitable environmental characteristics because of dispersal limitations). For the form of latitudinal gradients to remain invariant over time, (i.e., no changes in b_1 , b_2 , or other regression coefficients) changes in richness must be equal and additive at all latitudes, a highly unlikely phenomenon. Thus, we expect to see changing latitudinal gradients depending on the (1) magnitude of climate change at various latitudes, which is expected to be greatest at high latitudes (arctic amplification); (2) the response of species to gradients of land use conversion by humans, which historically was greater in temperate zones but is now proliferating most quickly in tropical habitats; and (3) the sensitivity of species to environmental changes, which is expected to be greatest for species occupying low latitudes (Tewksbury *et al.*, 2008; Wright *et al.*, 2009). All of this is compounded even more as climate change will also have indirect effects on the nature and strength of species interactions and community composition (Gilman *et al.*, 2005). Of course, increased habitat fragmentation and isolation will increase the likelihood of rates of extinction far exceeding rates of speciation and establishment, further altering geographic patterns of biodiversity as well as the spatial configuration of biodiversity into its hierarchical components (α -, β -, and γ -partitions).

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