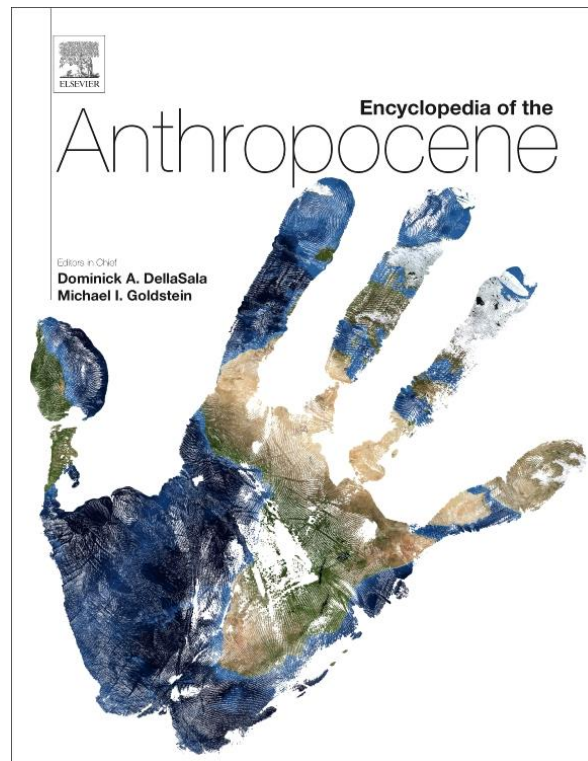


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Latitudinal Gradients of Biodiversity: Theory and Empirical Patterns

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What Are Latitudinal Gradients of Biodiversity?

Latitudinal gradients of biodiversity are biogeographic patterns that quantify the ways in which taxonomic, phylogenetic, functional, genetic, or phenetic biodiversity change with latitudinal position on the surface of the earth (Fig. 1). Historically, research has focused on gradients of species richness (i.e., the number of species in an assemblage) because that was the only information available to effectively evaluate patterns of biodiversity at broad spatial extents (Fig. 2). In general, species richness increases from polar to tropical regions (Willig et al., 2003; Hillebrand, 2004) for most taxonomic groups (e.g., mammals, birds, reptiles, amphibians, fish, tunicates, crustaceans, mollusks, brachiopods, corals, foraminiferans, and vascular plants) and geographical settings (e.g., Africa, North and South America, the Atlantic Ocean). In addition, species richness increases toward the tropics for many focal scales (Fig. 2), including those of broad climatic zones, arbitrary geographic subdivisions (e.g., latitudinal bands), and local ecological communities (Willig and Selcer, 1989; Kaufman and Willig, 1998; Stevens and Willig, 2002).

The form of the latitudinal gradient in biodiversity is not the same for all taxa or for all dimensions, with some groups (e.g., parasites, aquatic flora, North American wasps, marine birds, and mammals) or aspects (e.g., species evenness, species dominance, functional evenness) failing to increase toward the tropics (Willig et al., 2003). In addition, latitudinal gradients have not been consistent through time, being primarily restricted to the Paleozoic and the past 30 million years (i.e., times of colder climates). During warmer climatic periods, biodiversity peaked in temperate areas or latitudinal gradients were much less pronounced than they are currently (Mannion et al., 2014). Considerable debate continues about the relative importance of mechanisms that may contribute to latitudinal biodiversity gradients, with ecological, evolutionary, historical, and stochastic processes championed as the principal causes by different researchers (Table 1). Documenting global patterns of biodiversity, such as latitudinal gradients, and understanding the mechanisms that produce this spatial variation are critical steps in the design of global conservation strategies. This is of particular concern in the early 21st century with growing concern of an impending 6th mass extinction (Kolbert, 2015).

The Hierarchical Configuration of Biodiversity

The hierarchical configuration of biodiversity is a scale-dependent phenomenon that explicitly considers the relationship between patterns at local (α -diversity) and regional (γ -diversity) scales. Variation in species composition among local assemblages (β -diversity) is typically associated with habitat heterogeneity and contributes to the disparity between biodiversity at local and regional scales. An increase in regional species richness (γ -diversity) from polar to tropical latitudes can be a consequence of a gradient in species richness at the α -level (i.e., an increase in local biodiversity), the β -level (turnover in species composition among local communities), or a combination of the two. β -Diversity for species richness increases toward the equator for mammals, birds, shallow water bryozoans, trees, and herbaceous plants (Willig et al., 2003); however, the exact form of these relationships differs among taxa and biogeographic realms. For New World bats, the increase in local species richness (α -diversity) from extratropical to tropical communities is much less than that for regional species pools (γ -diversity), suggesting that β -diversity consistently increases toward the tropics (Fig. 2; Stevens and Willig, 2002). In contrast, β -diversity for species richness remained more or less constant below 30° N latitude for nonvolant mammals in North America (Kaufman, 1998) and did not contribute to latitudinal gradients of marsupial species richness in the New World (Willig and Gannon, 1997).

Dimensions of Biodiversity: A Case Study of New World Bats

Beyond species richness, taxonomic biodiversity has a number of other aspects such as evenness, diversity, and dominance. These aspects of taxonomic biodiversity weight the presence of species by measures of importance such as abundance, biomass, or frequency of occurrence. Evenness measures the extent to which individuals are equally distributed among species. Diversity is a composite metric that combines richness and evenness. Dominance is the extent to which a single taxon represents the largest proportion of individuals in an assemblage. A comprehensive analysis of latitudinal patterns of taxonomic biodiversity of New World bat communities based on 14 different indices representing species richness (three metrics), evenness (four metrics), dominance (three metrics), and diversity (four metrics) demonstrated that spatial variation in richness was independent of spatial variation in evenness (Stevens and Willig, 2002). Moreover, strong latitudinal gradients characterized bat species richness and diversity, but species evenness or dominance did not evince such gradients.

Latitudinal gradients in species evenness, diversity, or dominance, as well as in other dimensions of biodiversity (e.g., functional, phenetic, and phylogenetic), have received increasing attention since the turn of the century. The incorporation of functional and phylogenetic information has been particularly important for the evaluation of mechanisms that may contribute to these gradients.

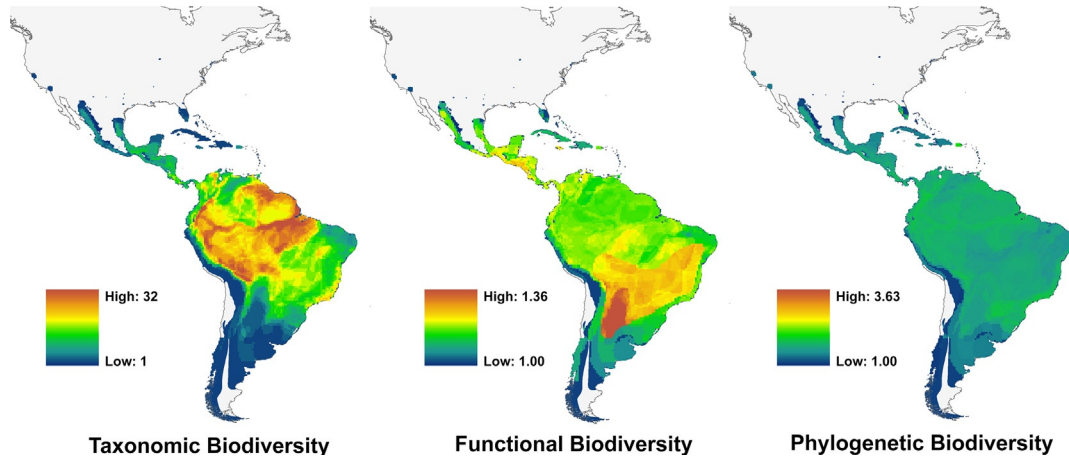


Fig. 1 Gradients of taxonomic (species richness), functional (Rao's Q; Botta-Dukát, 2005), and phylogenetic (Rao's Q) biodiversity for parrots in the New World. Modified from Burgio, K. R. (2017) Extinction, climate change, and the conservation of parrots: developing the models and tools needed to help save the world's most endangered order of birds. Ph.D. Dissertation, University of Connecticut, Storrs, Connecticut, USA.

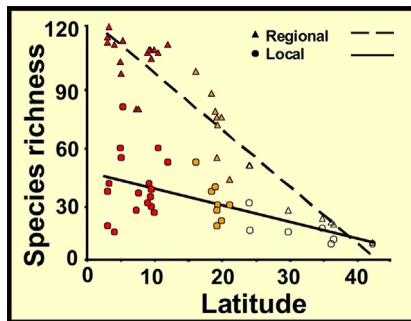


Fig. 2 Latitudinal gradients of local and regional species richness for New World bats. White, orange, and red dots correspond to temperate, subtropical, and tropical communities, respectively. Modified from Stevens RD and Willig MR (2002) Geographical ecology at the community level: perspective on the diversity of New World bats. *Ecology* 83: 545–560.

Table 1 Mechanisms potentially affecting the latitudinal gradient in species richness

<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

Modified from Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65: 514–527.

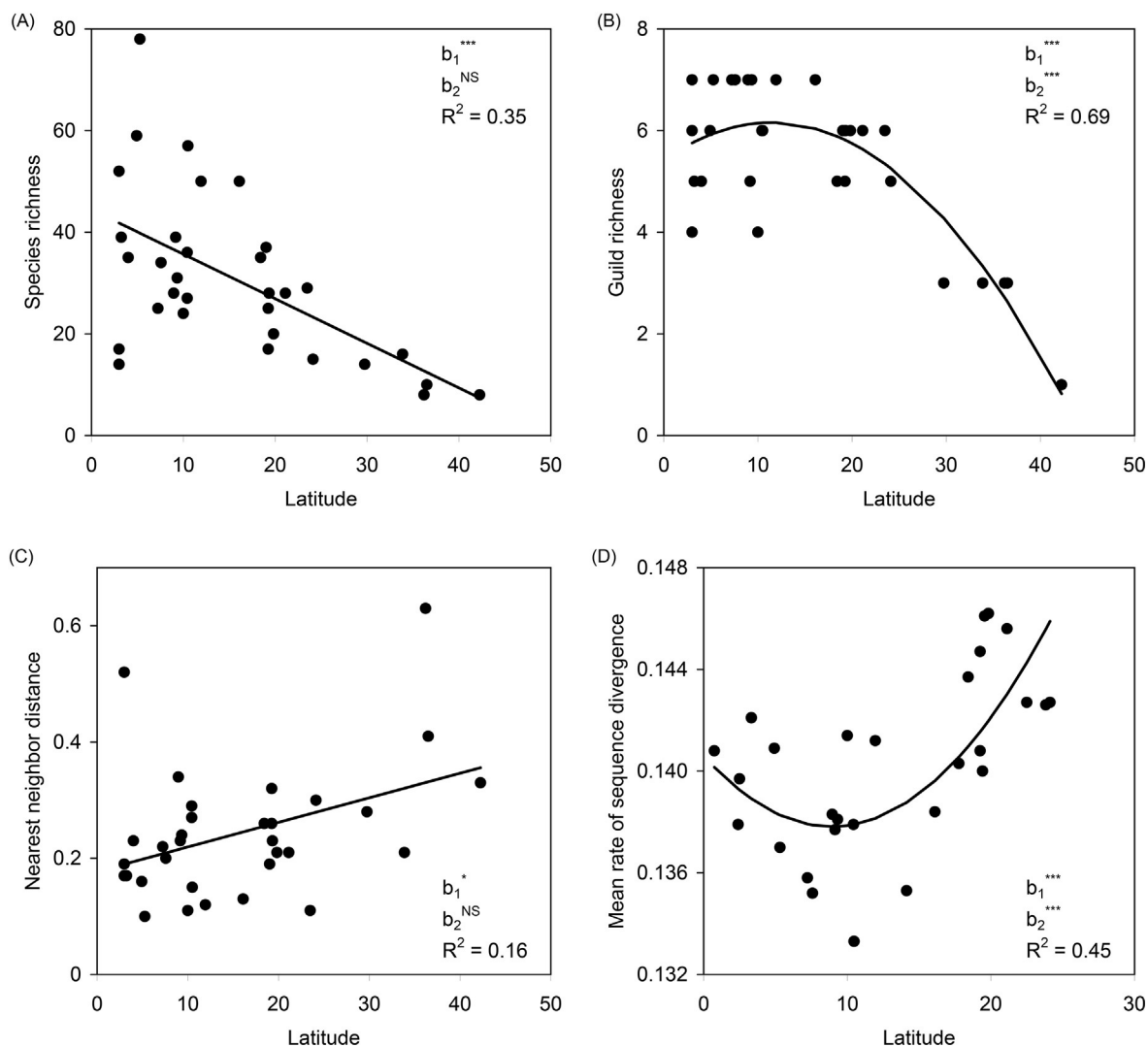


Fig. 3 Latitudinal gradient of taxonomic biodiversity (species richness, A), functional biodiversity (guild richness, B), phenetic biodiversity (nearest neighbor distance, C), and phylogenetic biodiversity (mean rate of sequence divergence, D) within local communities for bats from throughout the New World. *, ***, and NS indicate significant, highly significant, and nonsignificant linear or quadratic relationships with latitude. R^2 indicates the proportion of variation in biodiversity accounted for by each model. 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.

In general, gradients of functional, phenetic, and phylogenetic biodiversity have multiple forms (e.g., linear, quadratic, stochastic) and are not wholly a result of variation in species richness (Fig. 3). For example, latitudinal gradients of New World parrots are strikingly different for taxonomic, functional, and phylogenetic dimensions (Fig. 1): taxonomic biodiversity exhibits a classical equatorial peak, functional biodiversity is greatest in the subtropics both north and south of the equator, and phylogenetic biodiversity is low throughout the New World, having only a weak relationship with latitude.

Functional biodiversity evaluates variation in characteristics that relate to ecosystem processes, species interactions, or functional characteristics of a community. It can be evaluated based on the assignment of species to foraging guilds, such as frugivores, nectarivores, or insectivores, or based on the consideration of functional traits (e.g., aerodynamic characteristics, foraging locations, foraging strategies, dietary attributes). The latitudinal gradient of foraging guild richness of New World bats (Stevens et al., 2003) is strong, with guild richness increasing from extratropical to tropical latitudes; however, the form of the relationship is markedly nonlinear (Fig. 3B). Phenetic characteristics of species can reflect their ecological attributes and can be used to measure functional biodiversity. Such functional traits provide an integrated view of ecological relationships over space or time and represent a trait-based assessment of functional biodiversity. In contrast to gradients of species or guild richness, phenetic diversity of New World bats has a weak relationship with latitude and decreases slightly toward the tropics (Fig. 3C), indicating that species are slightly

more similar functionally as one approaches the equator (Stevens et al., 2006). This decrease in functional diversity indicates an increase in functional redundancy in bat assemblages toward the equator, possibly increasing functional resistance and resilience of these bat assemblages.

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 an assemblage). The latitudinal gradient of phylogenetic biodiversity for the Phyllostomidae (a clade of Neotropical origin) is different from that expected based on variation in species richness (Stevens, 2006). This arises because of the rate of sequence divergence of species in communities at tropical latitudes is less than that expected by random selection of species, whereas the rate of sequence divergence of species in communities at extratropical latitudes is greater than that expected by random selection of species. In general, the evolutionary histories of taxa influence the assembly of species into local communities, with the most derived and youngest taxa occurring farthest from the location of evolutionary origin.

Mechanisms

Many hypotheses (Table 1) posit mechanisms that contribute to latitudinal gradients of species richness. In general, these hypotheses make only qualitative predictions, with many hypotheses predicting similar spatial patterns. Most of the championed hypotheses represent conceptual models that provide insights into how natural processes could result in greater species richness toward the tropics but do not generate unique predictions that can differentiate among competing hypotheses or that can be applied to all dimensions of biodiversity. Rather than detail each hypothesis, we focus on a few that have generated considerable debate and insights into these spatial patterns.

Geographic Area Hypothesis

The latitudinal gradient of species richness may be a consequence of more area occurring in the tropics than in other geographical zones, as larger areas tend to harbor more species (Terborgh, 1973; Rosenzweig, 1995). Within large continental landmasses, the tropics comprise a single contiguous area, whereas northern and southern temperate or polar areas are separated by great distances. Moreover, environmental variation within the tropics is less than that in other geographical zones. A large area with relatively homogeneous climatic conditions in the tropics should lead to higher speciation rates and lower extinction rates compared to comparable areas in extratropical regions. Large tropical areas with similar environmental conditions allow species to have larger geographical ranges, which allow species to be represented by more or larger populations, diminishing the likelihood of stochastic extinction. In addition, larger areas are more likely to contain or experience geological events that produce geographic barriers that result in allopatric speciation. This combination of higher speciation and lower extinction rates should yield higher species richness in the tropics than in extratropical areas. Nonetheless, the positions, sizes, and configurations of the Earth's continents affect the proportion of land or water at each latitude, and these have varied through geological time.

The effect of area per se on latitudinal gradients of biodiversity is controversial. Because New World bats exhibit exceptionally strong latitudinal gradients of richness, they are a good test of the geographic area hypothesis (Willig and Bloch, 2006). Current ecogeographic zones (i.e., the geographical extent of a biome) of the New World are not larger in tropical compared to extratropical regions. Nonetheless, the latitudinal gradient of bat species richness is strong (Figs. 2 and 3A), indicating that area does not drive latitudinal patterns. In contrast, global vertebrate species richness in 32 biotic provinces supports the importance of area as a contributor to latitudinal richness gradients, with contemporary richness gradients linked to variation in historical area and productivity (Jetz and Fine, 2012).

Speciation, Extinction, and Diversification Rates

Many of the mechanisms (Table 1) proposed to explain latitudinal gradients in biodiversity can directly or indirectly affect rates of speciation and extinction. Speciation and extinction rates have been combined 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. The latitudinal gradient in diversification rates is thought to be driven primarily by temperature (Rohde, 1992). Warmer environments support shorter generation times, mutation rates increase as temperature increases and are highest in the tropics, and physiological processes are faster at higher temperatures. 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 biodiversity (Chown and Gaston, 2000; Fine, 2015).

Evidence suggests that diversification rates contribute to latitudinal gradients of species richness for vertebrates and for invertebrates from both terrestrial and aquatic ecosystems; however, evidence that diversification rates are the dominant mechanism is equivocal. Temperature affects speciation rates and contributes to the latitudinal gradient of species richness for planktonic foraminiferans (Escarguel et al., 2008) and swallowtail butterflies (Condamine et al., 2012). In contrast, there is no relationship between latitude and speciation rates in birds (Bromham and Cardillo, 2003). The effects of diversification rates on latitudinal gradients in mammal richness are complex. Speciation and extinction rates for the entire mammalian phylogeny are greater in the

tropics than in the temperate zone (Rolland et al., 2014), whereas many mammalian groups (e.g., primates, lagomorphs, Australasian marsupials, ungulates, shrews, bats, and rodents) have greater speciation rates or lower extinction rates in the tropics. In general, the relationship between temperature and species richness of mammalian clades is not positive (Buckley et al., 2010). Rather, niches are phylogenetically conserved within clades, and clades differ in climatic origin (i.e., clades of tropical origin may have positive temperature-richness relationships, but clades of temperate origin generally have negative temperature-richness relationships).

Recently, a single study (Jansson et al., 2013) used 111 phylogenies for mammals, birds, insects, and angiosperms to evaluate the relative support for three evolutionary hypotheses on the origin of latitudinal biodiversity gradients. The diversification rate hypothesis predicts greater speciation rates and lower extinction rates in the tropics. The “out-of-the-tropics” hypothesis (Jablonski et al., 2006) postulates that lineages originate in the tropics, diversify, and then disperse into temperate regions. The “tropical niche conservatism” hypothesis (Olalla-Tárraga et al., 2011) is based on the idea that lineages that originate in the tropics have difficulty adapting to extratropical climates, resulting in an accumulation of taxa that are restricted to tropical environs. Results supported the out-of-the-tropics hypothesis. Moreover, 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 be the primary drivers of latitudinal biodiversity gradients (Fine, 2015).

The Rapoport Effect

Rapoport's rule describes a pattern in which geographical ranges of species decrease in size from high to low latitudes. Smaller ranges could increase the number of species that occur at a latitude, producing latitudinal gradients at large spatial scales (e.g., for analyses based on latitudinal bands or ecogeographical zones). In temperate zones, an individual must be able to tolerate considerable seasonal variation in climate; thus, temperate species may have large distributions due to broad environmental tolerances. In contrast, an individual in the tropics experiences little seasonal variation in climate, suggesting that tropical species may be predisposed to have narrower environmental distributions. Nonetheless, little variation in climate characterizes a 50° wide latitudinal band centered on the equator, allowing tropical species to have large geographical ranges without adapting to a wide range of climatic conditions. To span a similar latitudinal range, extratropical species must adapt to a temperature range of 37.5°C, spanning latitudes from the subtropics into the Arctic Circle (e.g., from 25° to 75°). Consequently, it is unclear how a lack of seasonality in the tropics would restrict the range sizes of species in a large contiguous and climatically invariant region.

The Rapoport effect is documented for mammals, reptiles, amphibians, fish, crayfish, amphipods, mollusks, and trees and was quickly accepted as the explanation for latitudinal gradients in species richness in ecology textbooks. Additional support was derived from the fact that taxa that do not adhere to Rapoport's rule also do not increase in richness toward the equator, suggesting that both patterns were derived from the same mechanism (Stevens, 1989). Nonetheless, a growing body of evidence demonstrates that the Rapoport Effect is not universal: New World bats and marsupials (Lyons and Willig, 1997; Willig and Lyons, 1998), marine teleosts (Rohde et al., 1993), and Pacific mollusks (Roy et al., 1994) each exhibit strong latitudinal gradients in diversity but do not adhere to Rapoport's rule, indicating these two patterns may not have a shared cause. A comprehensive set of simulation models provide added insight into the evaluation of Rapoport's rule (Taylor and Games, 1999). These models suggest that the Rapoport effect would create a richness gradient that is opposite of the pattern found in nature, with species richness increasing with increasing latitude. Only the incorporation of ecological responses to factors other than climate in the simulation model produces latitudinal gradients consistent with real-world patterns. For example, habitat size and topographic complexity affect latitudinal gradients in range size more so than the climatic basis for the Rapoport rule (Hawkins and Diniz-Filho, 2006).

Geometric Constraints Hypothesis

Geographic constraints may affect patterns of species distribution within a domain, creating modal patterns with peak richness in the middle of the domain (Colwell and Hurtt, 1994; Willig and Lyons, 1998; Colwell and Lees, 2000). This hypothesis would consider peak species richness in the tropics to be a consequence of the bounded nature of habitable zones on earth (i.e., area between the two poles). Species richness of a biota should increase toward the center of a shared geographic domain as a consequence of the random placement of species ranges within that domain (Colwell and Hurtt, 1994; Willig and Lyons, 1998). Other mechanisms proposed to account for latitudinal gradients only suggest qualitative increases in richness with decreasing latitude. In contrast, geometric constraint models make both qualitative and quantitative predictions concerning the form (quasiparabolic or parabolic) of the latitudinal gradient, allowing comparisons of predicted and empirical values (Pineda and Caswell, 1998; Willig and Lyons, 1998; Lees et al., 1999).

Considerable debate exists about the application, utility, and interpretation of geometric constraint models (e.g., Colwell et al., 2004, 2005; Zapata et al., 2003, 2005; Hawkins et al., 2005). Importantly, these models provide baseline expectations for gradients of species richness in the absence of ecological or evolutionary mechanisms. Nonetheless, geometric constraint models are most likely to provide insights when the axis of constraint (e.g., latitude, elevation, ocean depth) is associated with important environmental gradients, such that deviations from predictions suggest possible causal mechanisms.

Summary

The theory of latitudinal gradients of biodiversity has matured considerably during the past 20 years, with the addition of functional and phylogenetic perspectives (Fig. 1) representing important advancements for understanding the relative contributions of historical and contemporary processes to these global patterns. Gradients of species richness are stronger and steeper for regional biotas than for local communities and are similar in northern and southern hemispheres (Fig. 2). In addition, relationships in marine and terrestrial environs are stronger and steeper than those in freshwater environs.

The manner in which particular mechanisms contribute to biogeographic patterns of biodiversity is becoming clearer, with this understanding being used to provide insights about other types of biodiversity gradients (e.g., elevation, ocean depth, productivity). In addition, latitudinal gradients are being integrated with other broad-scale patterns to better understand how particular ecological or evolutionary mechanisms affect spatial patterns of biodiversity. The past decade has seen renewed interest in how evolutionary and historical mechanisms shape contemporary biogeographic patterns. From an ecological perspective, understanding the degree to which area, climatic variability, productivity, temperature, and their interactions mold gradients of biodiversity remains a challenge.

The theory and mechanisms for latitudinal gradients of functional or phylogenetic biodiversity are in the early stages of development, and the generality of the forms of their latitudinal patterns are not well established. Nonetheless, latitudinal gradients in these dimensions are not wholly explicable by variation in species richness and historical factors likely play an important role in shaping these gradients.

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