

LATITUDE, COMMON TRENDS WITHIN

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- I. Context
 - II. Patterns
 - III. Mechanisms
 - IV. Amplification and Synthesis
 - V. Assessment
-

GLOSSARY

alpha diversity The diversity of species, often estimated as species richness, within a local community or site.

beta diversity The degree of turnover in species (and changes in their abundances) among communities or sites along a gradient or within a larger area.

gamma diversity The diversity of species, often estimated as species richness, in a larger area as a consequence of both alpha and beta diversity.

latitudinal gradient A gradual change in a characteristic of interest (e.g., species richness) 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 latitudinal extremes to the middle of a region as a consequence of the random placement of species ranges within a geographic domain (also known as Perinet effect).

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 attributes.

species density The number of species within a sampling unit of fixed size.

species diversity A feature of biological communities or assemblages 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 The total number of species in an area.

LATITUDINAL gradients of diversity are biogeographic patterns that define the way in which the number of species changes with latitudinal position on the surface of the earth. The general pattern is for species richness to increase from polar to tropical regions (Brown, 1995; Gaston, 1996; Rosenzweig, 1995), regardless of the taxonomic affiliation of the 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 those organisms alive during the past 70 million years (Fig. 2). An increase in species richness with decreasing latitude is the pattern generally observed at three spatial scales, including the level of

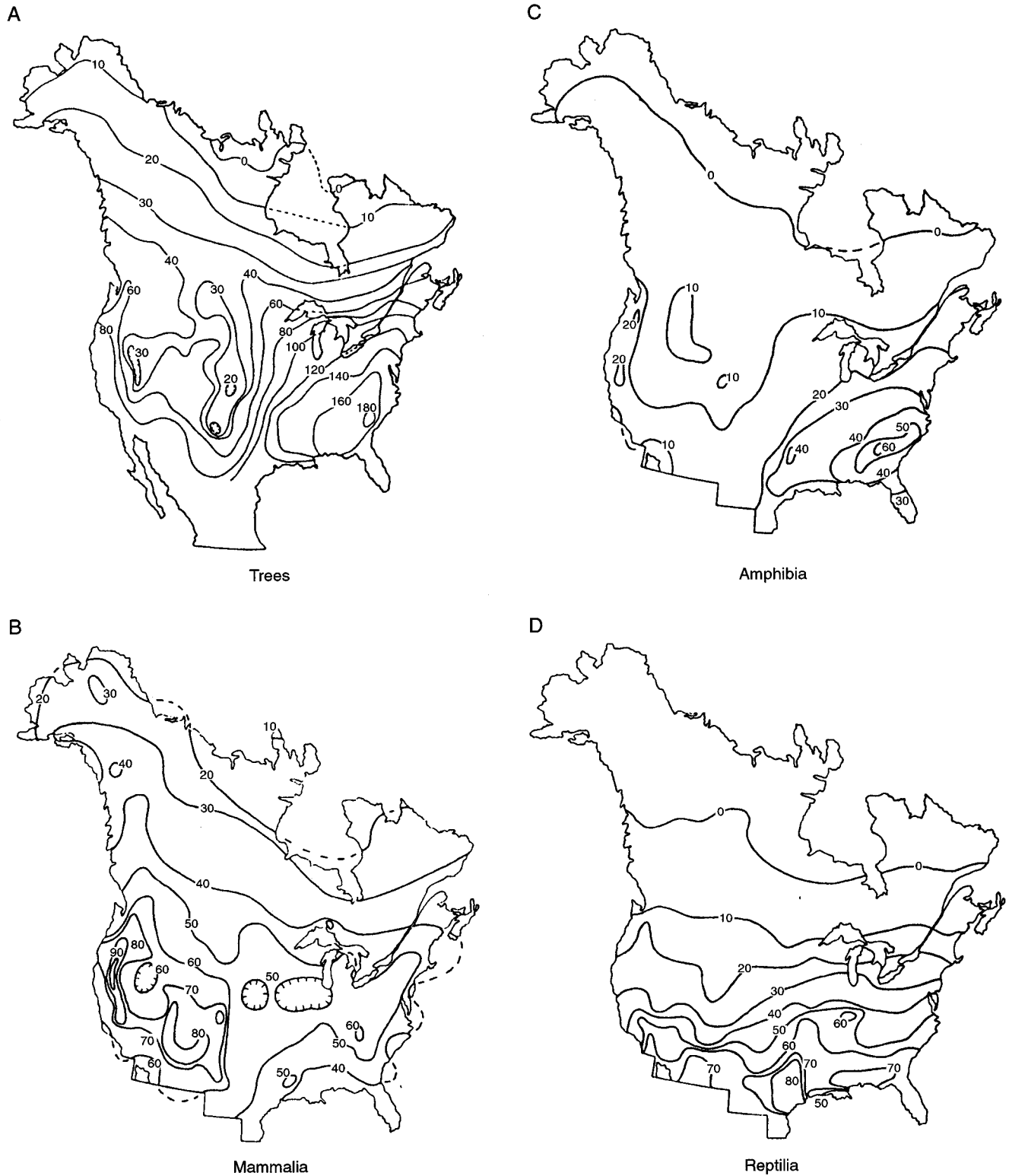


FIGURE 1 Species richness gradients in Canada and the United States for trees (A), mammals (B), amphibians (C), and reptiles (D). Contour lines connect localities with approximately equal species richness (reproduced from Currie, 1991, with permission from The University of Chicago Press).

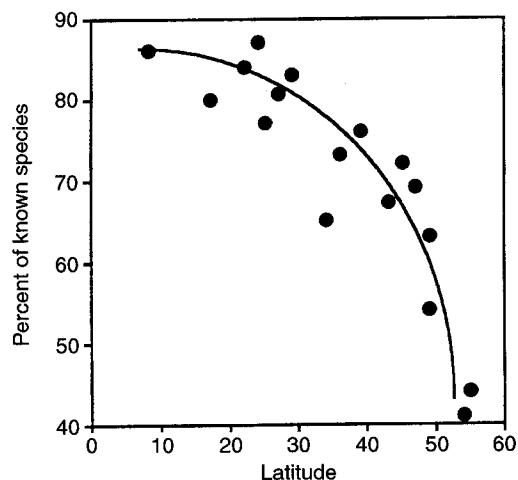


FIGURE 2 Latitudinal gradient in fossil species richness for marine Foraminifera from approximately 70 million years ago (modified from Rosenzweig, 1995).

broad climatic zones (Fig. 3), assemblages occupying arbitrary geographic subdivisions (i.e., quadrats or bands) of the earth's surface (Fig. 4), and local ecological communities (Figs. 4 and 5). Nonetheless, not all taxa increase with latitude in the same fashion, and a

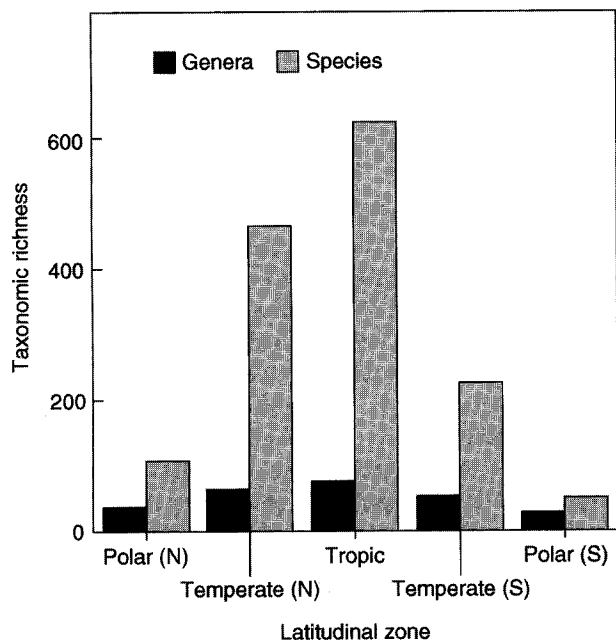


FIGURE 3 Generic and species richness of tunicates in each of five major climatic regions defined by latitude and arranged from northern-most latitudes, through the tropics, to southern-most latitudes (modified from Fischer, 1960).

few groups do not even exhibit the general pattern of a latitudinal increase in richness. Moreover, considerable controversy surrounds the mechanisms that affect latitudinal patterns in diversity, with ecological, evolutionary, historical, and stochastic processes (Table I) championed as the cause(s) of observed gradients (Rhode, 1992). Indeed, many of the mechanisms are circular or unsubstantiated by empirical data.

I. CONTEXT

Since the voyages of Darwin and Wallace, biologists have been fascinated with the high species diversity of tropical regions compared to those in temperate or boreal zones. Indeed, this fascination with tropical diversity catalyzed in many ways the conceptual development of the theory that currently constitutes modern ecology. Moreover, increasing concern about the loss of diversity, especially in tropical regions, has led to the rapid development of the science of conservation biology. Documenting the way in which diversity differs 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). Within the next 25 years, scientists convincingly had documented the ubiquity of gradients in which species richness increased toward tropical areas. Similar gradients also were documented for diversity of higher taxonomic groups (e.g., genera, families, and orders) (Figs. 3 and 4). Indeed, the increase in species richness for terrestrial and marine environments was quantified successfully for a wide variety of taxonomic groups, such as mammals, birds, reptiles, amphibians, fish, tunicates, crustaceans, mollusks, brachiopods, corals, foraminiferans, and vascular plants. Nonetheless, some taxa representing lower levels in the systematic hierarchy (i.e., orders or families) were notable exceptions in having maximal diversity in polar (e.g., seals, penguins, and sandpipers) or temperate zones (e.g., voles, salamanders, ichneumonid wasps, and coniferous trees). 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.

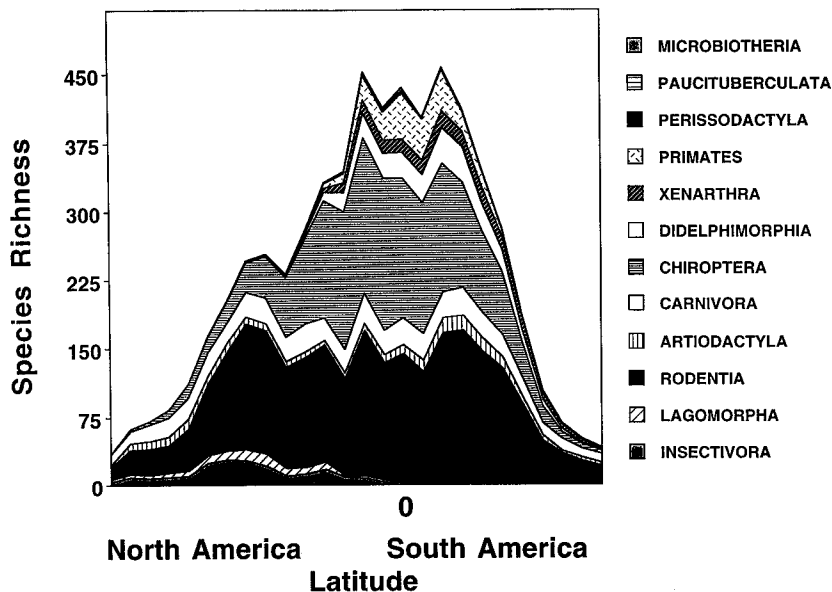


FIGURE 4 Differential contribution of mammalian orders to the latitudinal gradient of species richness in the New World based on data from 5-degree latitudinal bands (after Kaufman, 1995).

II. PATTERNS

A gradient implies a gradual change in species richness with a gradual change in latitude. In an unambiguous fashion, the form of that pattern is the precise mathematical or statistical relation that describes how species richness 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 relation, 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 versus mammals versus reptiles versus amphibian in North America) as well as comparisons among different geographic domains for the same taxon (Fig. 4; North American versus South American for mammalian orders).

Patterns are often scale dependent, with particular mechanisms more likely operating at some areal scales than at others. Consequently, patterns will be elucidated for each of two foci: biotic assemblages occupying broad areas and ecological communities occupying local sites. These scales are intimately associated with

each other. In part, the diversity of regions, biomes, or climatic zones is a consequence of the species richness that is accumulated within 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).

A. Assemblages

Most of the empirical research concerning the relationship between species richness and latitude that has been done using arbitrary sampling units has been based on (i) latitudinal bands, (ii) quadrats of fixed area, or (iii) 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 area of any sampling unit may have as large or larger an effect on variation in species richness than does its latitude, it is critical to understand how area may affect latitudinal patterns in different ways, depending on the method or approach.

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 quantitative conclusions. As meridians converge toward the poles, the size of the

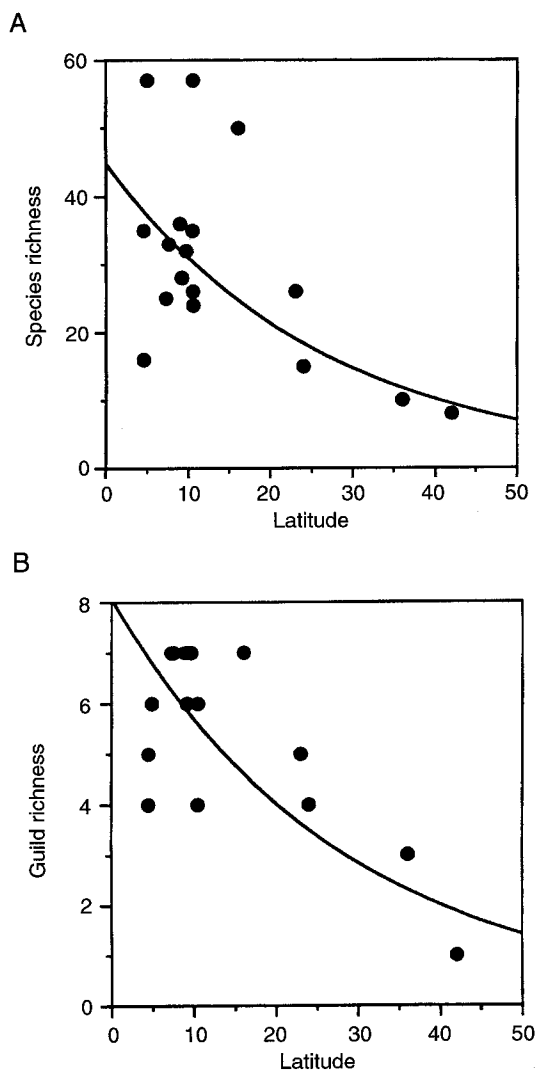


FIGURE 5 Latitudinal gradient of species richness (A) and feeding guild richness (B) within local communities for bats from throughout the New World (based on Stevens and Willig, 1999).

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 detection of pattern 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 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-degree 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 taken to adjust species richness in accord with 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. That is, the pattern detected for quadrats encompassing 100 km² could be quite different from those at 10,000 km². The importance of scale dependence in ecology and biogeography has been emphasized increasingly during the past decade. Nonetheless, broad-scale biogeographic patterns for sampling units between 1000 and 25,000 km² have been shown recently to be scale independent and little affected by area (Lyons and Willig, 1999).

Much of the early literature on latitudinal gradients in diversity 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, and 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,

TABLE I
Mechanisms Potentially Affecting the Latitudinal Gradient in
Species Richness^a

Circular	Empirically unsubstantiated
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

^a Modified from Rohde (1992).

ant species the Americas, and breeding bird species 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, suggesting that latitudinal correlates other than area are the driving forces behind the gradient.

B. Ecological Communities

The way in which latitudinal variation in diversity at broad spatial scales (gamma diversity) is related to patterns of species richness at the level of local communities (alpha diversity) 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 local communities in tropical regions, making assessment of broad-scale latitudinal patterns of community richness a premature endeavor.

Finally, it is unlikely that a single research scientist could gather sufficient data across many sites to assess latitudinal gradients in community richness with sufficient power to distinguish pattern from noise. 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. The concern expressed by Voss and Emmons (1996) regarding adequate sampling within a community 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 they must be constrained to some extent by both time and space. Sampling regimes which 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 interaction, it becomes clear that species richness increases from polar

through temperate to tropical regions. The gradient can arise from an increase in the number of functional groups (e.g., guilds or ensembles) within a community as well as from an increase in the number of species per functional group. For example, data for volant mammals (bats) from 17 local communities (Stevens and Willig, 1999) 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. 5A). A similar increase in the number of functional groups or feeding guilds within a community (Fig. 5B) contributes to this trend. Specifically, north temperate bat communities are depauperate with 10 or fewer species, all of which are members of carnivorous feeding guilds (e.g., aerial insectivore, molossid insectivores, or gleaning animalivores). In contrast, tropical and subtropical communities on average contained 33.7 and 20.5 species, respectively. Moreover, functional diversity of communities in these two regions was high (equaling 5.9 and 4.5 feeding guilds, respectively) and included sanguivorous, piscivorous, frugivorous, and nectarivorous taxa in addition to the guilds represented in the temperate communities.

Species richness of nonvolant taxa (tetrapods) in mammalian communities from North America also shows a significant increase from polar to tropical regions (Fig. 6; Kaufman, 1998). Tropical communities contained approximately 45.5 species on average, whereas extratropical communities contained only approximately 25.8 species. Within these two latitudinally defined climatic regions, the relationship between richness and latitude was nonsignificant. Most important, an examination of species turnover for these communities revealed that beta diversity increased toward the tropics as well. Hence, increasing diversity of broad geographic or climatically defined regions (gamma diversity) with decreasing latitude may be a consequence of the increase in local diversity (alpha diversity) as well as the increase in differentiation among local communities within latitudinal regions. This appears to be the case for nonvolant mammals in the New World, at least at some spatial scales.

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 such as competition in molding community attributes. Subsequent focus on the distinction between equilib-

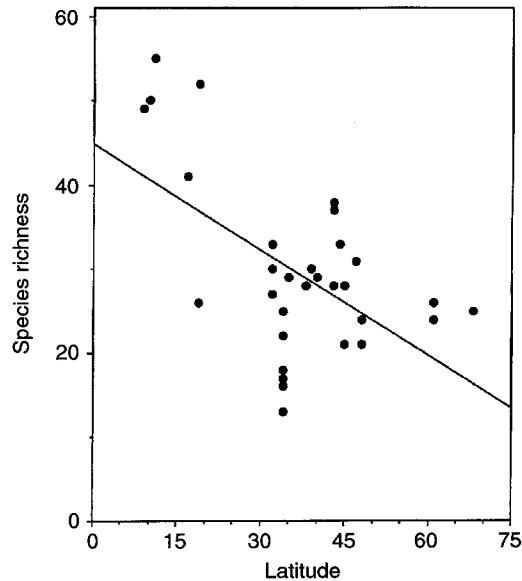


FIGURE 6 Latitudinal gradient of species richness for mammalian tetrapods in local communities in North America (based on Kaufman, 1998).

rial and nonequilibrium 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 equilibrium richness may contribute strongly to the latitudinal gradient in diversity (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 favor high diversity. To the extent that high solar insolation and warm temperatures represent favorable conditions, 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, the factors that affect elevated richness at the local scale likely contribute to enhanced gamma diversity of regions as well (see Section IV).

III. MECHANISMS

A grand proliferation of hypotheses (Table I), along with subsequent a posteriori modifications, is a characteristic feature of the literature concerning the relationship between diversity and latitude. A variety of factors contribute to this. Each of these hypotheses 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, almost all hypotheses provide only a general qualitative prediction that richness should increase toward the tropics. The hypotheses represent conceptual models that lend insight into how nature could operate but do not generate unique predictions based on direct features of the gradient that allow conclusive elimination of competing hypotheses in the sense of strong inference. Moreover, many hypotheses are circular in nature and the indirect predictions that they make about latitudinal gradients have not been examined from an empirical perspective. In addition, some hypotheses only pertain to specific taxa or ecological groups so that they are not applicable universally.

Rather than elucidate 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 which have generated debate in the contemporary literature follows. These hypotheses represent areas of research which likely will contribute to the complexion of the discipline in the future.

A. 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) in subsequent years, during which the effects of productivity and zonal bleeding have been incorporated 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.

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 intermeridian 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 in tropical versus extratropical regions, 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 (torrid, temperate, and polar) reveals that the tropics ranks second in area to north 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 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 resulting from

accidental cause or from environmental perturbation. Simultaneously, larger areas are more likely to contain or experience geological events that produce geographic barriers that enhance the rate of allopathic speciation. The dynamic balance between the rates of speciation and extinction therefore yield higher equilibrium richness in the tropics than in extratropical areas (Fig. 7).

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 increases 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. 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. Clearly, consensus is elusive concerning the relative importance of area in affecting species richness compared to other mechanisms.

B. Evolutionary Speed

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 homiotherms and poikilotherms. Second, mutation rates increase as temperature increases and are highest in the tropics. Third, faster physiological processes occur 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.

Much of the subsequent dialog concerning the evolutionary speed hypothesis has been embedded in the debate concerning the efficacy of area, productivity, and zonal bleeding in producing empirical gradients of diversity with respect to latitude. Although this debate has been fruitful in crystallizing assumptions of equilibrium conditions and species saturation as they relate to the area hypothesis, it has not furthered our understanding of the possible role of temperature in effecting higher speciation rates. Rhode has challenged the research community with this supposition; unfortunately, the response is deafening in its silence.

C. 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 recently has come to the forefront of the macroecological literature (Stevens, 1989, 1992) and been termed Rapoport's rule after the Argentine scientist who first discussed the pattern in the context of many other areographic principles. Stevens hypothesized that the latitudinal propensity for range size to decrease toward the tropics, when combined with differential movement

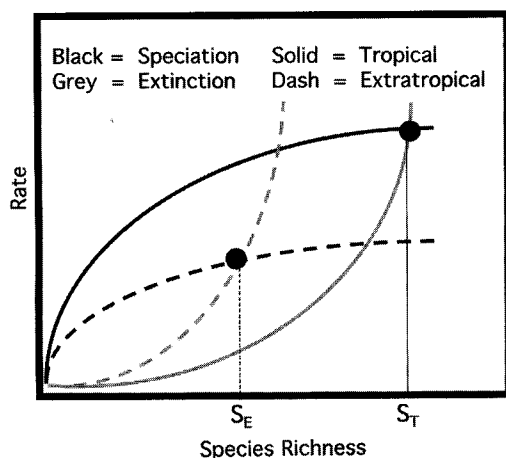


FIGURE 7 Graphical model illustrating the dynamic equilibrium between rates of speciation and extinction for tropical and extratropical latitudes (modified from Rosenzweig, 1995).

of individuals from source to sink habitats (rescue or mass effect), 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.

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 source or high-quality 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 differentially inflates species richness in tropical areas, generating the latitudinal gradient 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, is 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 has become engrained as the explanation for species diversity gradients in a variety of ecology textbooks. Additional circumstantial evidence was derived from the observation that taxa, which do not show the general latitudinal gradient in richness, 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 pattern is far from universal (Rohde *et al.*, 1993; Lyons and Willig, 1997). Moreover, reanalyses 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.

Recent 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 Gaines, 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 still fails to rescue the hypothesis; the predicted pattern remains a decrease in richness toward the tropics. Only the incorporation of competitive effects to either 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.

D. Geometric Constraint Hypotheses

The ubiquity of the latitudinal increase in diversity with decreasing latitude stimulated the search for a predominant mechanism effecting variation in richness. The rationale was essentially that because almost all taxa on all continents as well as in the oceans followed the same pattern, and the pattern has persisted through geological time, a single mechanism must be causing it. Interestingly, the search for a predominant mechanism during the past 25 years has generated increasingly more hypotheses rather than leading to consensus or a synthetic understanding of mechanisms producing the universal pattern.

Insights during the past 5 years concerning the nature of geographic constraints in affecting patterns of species distribution document clearly that modal patterns of diversity peaking in the tropics can be a consequence of the bounded nature of terrestrial and aquatic habitats. Indeed, both simulation (Colwell and Hurtt,

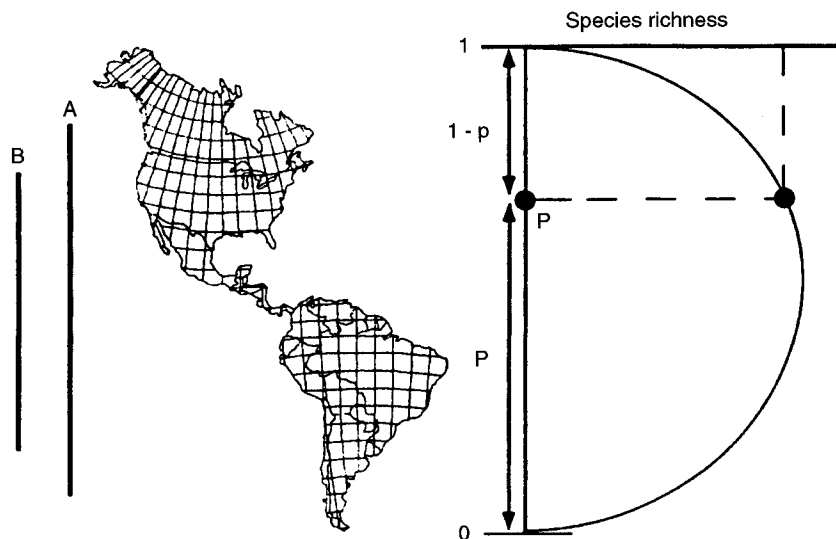


FIGURE 8 Graphical representation (parabola) of the gradient of species richness that arises from the random placement of species ranges within the latitudinal bounds of the New World, scaled from 0 in the south to 1 in the north (modified from Willig and Lyons, 1998). The number of species at any latitude 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.

1994; Pineda and Caswell, 1998) and analytical (Lees *et al.*, 1999; Willig and Lyons, 1998) null models suggest that species richness of a biota should increase toward the center of a shared geographic domain in a quasi-parabolic or parabolic fashion as a consequence of the random placement of species ranges [the mid-domain effect of Colwell and Lees (1999)]. Three null models have been developed that differ in the manner in which species ranges are randomized. Unlike the other mechanisms proposed to account for latitudinal gradients, which only suggest qualitative increases in richness with decreasing latitude, 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.

In the fully neutral model (Colwell and Hurtt, 1994; Willig and Lyons, 1998), the placement of termini for each species distribution is random, with the geometric constraint that they occur within a shared boundary or domain. As a consequence, the number of species at any point within the domain (S_p) is only related 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 $S_p = 2p(1 - p)S$. The model (Fig. 8) is an incarnation of both the two-hit broken stick model of MacArthur 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

$$\text{Pr}(P) = 1 - p^2 - (1 - p)^2 = 2p - 2p^2,$$

where p^2 is the proportion of species whose northern and southern boundaries lies 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 $\text{Pr}(P) = 2p - 2p^2$ is a parabola that peaks at 0.5, and as a consequence the average size range of species in the biota is half the extent of the domain (0.5).

The other two models have constraints concerning either the range size distributions of the biota or the distributions of midpoints within the domain. In the second model, the placement of ranges within the domain is constrained such that the simulated ranges have a size distribution exactly equal to that of the biota of interest. Essentially, the size of a species range limits the options for the feasible placement of midpoints: Species with broad distributions must have midpoints located near the center of the domain, whereas species with increasingly narrow ranges can have midpoints

located ever more distant from the center of the domain. Hence, randomization of location for the midpoint of each species range is constrained to only occur within a subset of the domain, and within this subdomain its position is determined from a uniform random distribution. This produces a quasi-parabolic curve that becomes increasingly flattened as mean range size diverges from 0.5 (the mean value in the totally null model). The third model constrains the distribution of midpoints to be exactly the same as that in the empirical data. It essentially allows the extent of each species range to vary in a uniform random manner with the only constraint being that its distributional midpoint not change. Although it exists as a simulation null model, its analytical analog has not been developed (Colwell and Lees, 1999).

Empirical support for geometric constraints is limited but increasing. In a comparison of empirical latitudinal gradients of richness with predictions of a geometrically constrained null model in the New World, Willig and Lyons (1998) were able to account for 69–95% of the variation in species richness for bats and marsupials (Fig. 9). Nonetheless, systematic deviations from the null distribution were observed for both taxa. The null model overestimated bat species richness near the edges of the domain and underestimated richness near the center of the domain. In contrast, the null model consistently overestimated species richness for marsupials at all latitudes. Although both taxa gradually increase in species richness toward the tropics, the manner in which they deviated from the predictions of the null model is in sharp contrast, and the residuals were not related to the area or the width of the continent at each latitude.

The geometric model constrained to conform to empirical range size distributions accounted for the spatial distribution of endemic rain forest taxa (e.g., butterflies, frogs, rodents, tenrecs, chameleons, and birds) in Madagascar far better than did mechanisms related to area, elevation, temperature, precipitation, habitat diversity, or productivity (Lees *et al.*, 1999). Richness peaked at or near the midpoint of domains even though values for numerous environmental characteristics did not do so. This was true for the one-dimensional domain of latitude (the model accounts for 85% of variation in richness) as well as for the two-dimensional domain defined by latitude and longitude (the model accounts for 75% of the variation in richness).

In an analogous fashion, applications of geometric constraint models to elevational distributions of birds (Rahbek, 1997) or bathymetric distributions of gastropods and polychaetes (Pineda and Caswell, 1998) have

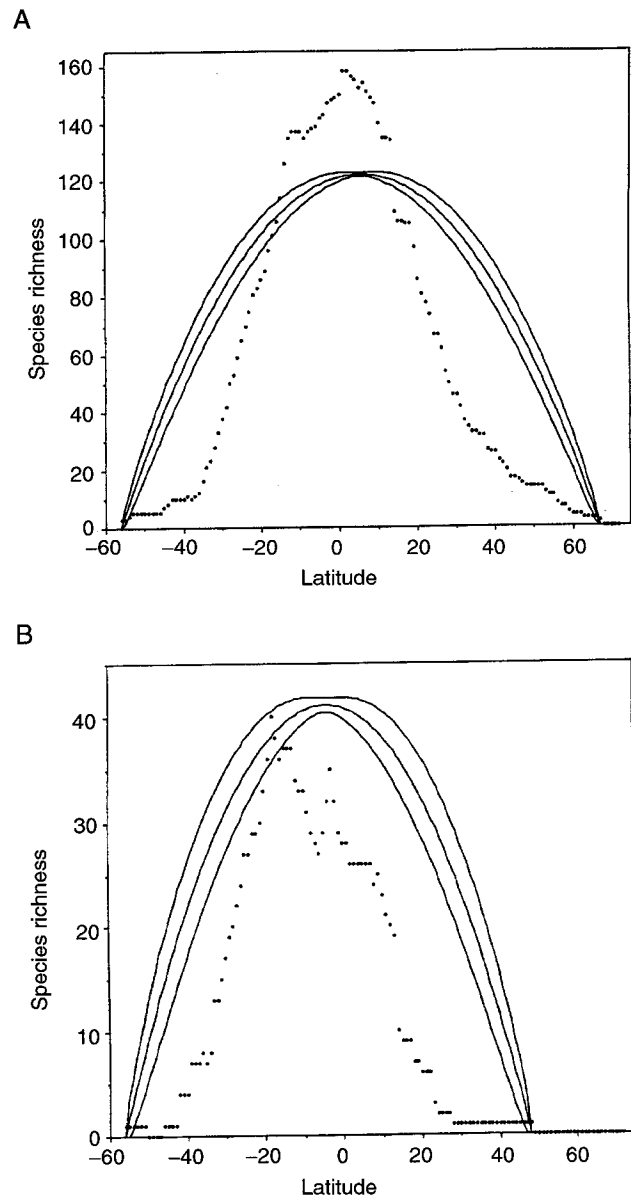


FIGURE 9 Comparison of the empirical latitudinal gradient of species richness (dots) with the predicted values (outer lines represent 95% confidence bands, and inner line represents predicted value) generated by a null model constrained only by the distributional bounds of the fauna for bats (A) and marsupials (B) in the New World (modified from Willig and Lyons, 1998).

led to considerable insight concerning diversity gradients. This is particularly relevant because elevational gradients are thought to recapitulate latitudinal patterns and mechanisms. For New World tropical birds, a peak in species richness occurred at an intermediate elevation, after controlling for the effects of area. Indeed,

a geometric model without constraints related to the elevational distribution of midpoints or extents, rather than other hypotheses, accounted for a significant amount of the elevational variation in species richness. Nonetheless, the actual midelevational peak in richness was depressed compared to the exact midelevation. In contrast, a similar model applied to marine invertebrates in the North Atlantic failed to account for salient features of the bathymetric gradient in richness. Although the location of a midgradient peak in richness did correspond between the model and the empirical pattern for gastropods, the model failed to account for the curvature and kurtosis of the empirical diversity gradient. For polychaetes, the model predicted the value for maximal richness. Nonetheless, the location of the peak along the depth gradient and the curvature of the relationship did not correspond between empirical data and model predictions.

Clearly, geometric constraints rather than evolutionary, environmental, or historical factors can produce latitudinal gradients that share many quantitative features with empirical patterns. Random processes may predispose various biotas to produce gradients with peaks in richness at midlatitudes. The challenge to macroecology is to understand the mechanisms that result in deviations from such null models, as well as to account for peaks in diversity and define the form of the diversity–latitude relationship *per se*.

IV. AMPLIFICATION AND SYNTHESIS

Based on first principles, Kaufman *et al.* (2000) provided a synthetic model to explain the latitudinal gradient in diversity based on variation in abiotic stress, productivity, and biotic interactions. The model is comprehensive because it simultaneously considers and makes predictions about other macroecological patterns, such as latitudinal gradients in range size, habitat specificity, and species dominance. Central to their model is the premise that abiotic stress increases with increasing latitude. The stress is a result of three interacting phenomena that vary with latitude as a consequence of the spherical nature of the earth and the fact that it rotates on a tilted axis with respect to the sun. Solar radiation is the ultimate source of energy for all food webs, and the daily input of energy per unit area decreases from the tropics to the poles. Similarly, the two essential metabolic pathways that dictate energy transformation in the earth's living systems—photosynthesis and respiration—are temperature dependent, and average daily temperature decreases from

tropical to polar latitudes, increasing the costs of executing all life-sustaining physiological processes. Finally, intra-annual variation in both temperature and solar insolation increases from tropical to polar regions. Together, these phenomena result in increasingly energy-poor and stressful environments toward high latitudes which reduces the richness of local communities and assemblages. Increased costs of maintaining metabolic rates combined with reduced inputs of energy in extratropical regions result in population densities of a species diminishing at high latitudes, whereas increased biotic pressures resulting from interspecific interactions reduce densities at the tropical edge of a species boundary. Consequently, species are expected to have modal geographic distributions of population size. Second-order biotic feedbacks (e.g., parasitism, disease, and diffuse competition) are hypothesized to further increase the costs of survival where richness is high, thereby truncating the extent of species distributions and the abundance of local populations in tropical regions. This would generate a Rapoport effect and increase the rate of species turnover (beta diversity) and diminish dominance toward the tropics. Although data are insufficient to test all of the patterns predicted by the synthetic model, and there is controversy surrounding the ubiquity of the Rapoport effect, for heuristic reasons alone the conceptual model provides a springboard from which enhanced understanding of the causes and consequences of the latitudinal gradient may be forthcoming.

V. ASSESSMENT

The ontogeny of theory can be viewed from a variety of perspectives that deal with the detection of patterns, the linkage of patterns to particular mechanisms, and ultimately the integration of those constructs to other theories in the discipline (Pickett *et al.*, 1994). The theory of latitudinal gradients of diversity has matured considerably in the past 5 years. The general patterns of latitudinal increase are well documented from an empirical perspective. In addition, the manner in which particular mechanisms could affect patterns of diversity has become clearer. Elements of the theory have been used to understand other gradients of diversity, such as those related to elevation or depth. Finally, latitudinal patterns of diversity 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. This represents a significant advancement in understanding and integration.

Although few of the hypotheses postulated to affect the latitudinal gradient in diversity 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 variability or stress, geographic constraints, productivity, temperature, and their interactions mold the latitudinal gradient in diversity remains a challenge for the next decade of scientists to address in a synthetic manner.

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Bibliography

- Brown, J. H. (1995). *Macroecology*. Univ. of Chicago Press, Chicago.
- Colwell, R. K., and Hurtt, G. C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *Am. Nat.* 144, 570–595.
- Colwell, R. K., and Lees, D. C. (1999). The mid-domain effect: Geometric constraints on the geography of species richness. Submitted for publication.
- Currie, D. J. (1991). Energy and large-scale patterns for animal- and plant-species richness. *Am. Nat.* 137, 27–49.
- Fischer, A. G. (1960). Latitudinal variations in organic diversity. *Evolution* 14, 64–81.
- Gaston, K. J. (Ed.) (1996). *Biodiversity: A Biology of Numbers and Difference*. Blackwell, London.
- Kaufman, D. M. (1995). Diversity of New World mammals: Universality of the latitudinal gradients of species and bauplans. *J. Mammal.* 76, 322–334.
- Kaufman, D. M. (1998). The structure of mammalian faunas in the New World: From continents to communities. Unpublished doctoral dissertation, University of New Mexico, Albuquerque.
- Kaufman, D. M., Sax, D. F., and Brown, J. H. (1999). The latitudinal diversity gradient: Toward a unified theory. Unpublished manuscript.
- Lees, D. C., Kremen, C., and Adriamampianina, L. (1999). A null model for species richness gradients: Bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biol. J. Linnean Soc.* 67, 529–584.
- Lyons, S. K., and Willig, M. R. (1997). Latitudinal patterns of range size: Methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos* 79, 568–580.
- Lyons, S. K., and Willig, M. R. (1999). A hemispheric assessment of scale-dependence in latitudinal gradients of species richness. *Ecology*, 2483–2491.
- Pickett, S. T. A., Kolasa, J., and Jones, C. A. (1994). *Ecological Understanding: The Nature of Theory and the Theory of Nature*. Academic Press, San Diego.
- Pineda, J., and Caswell, H. (1998). Bathymetric species-diversity patterns and boundary constraints on vertical range distributions. *Deep-Sea Res. II* 45, 83–101.
- Putman, R. J. (1994). *Community Ecology*. Chapman & Hall, London.
- Rahbek, C. (1997). The relationship between area, elevation and regional species richness in Neotropical birds. *Am. Nat.* 149, 875–902.
- Rohde, K. (1992). Latitudinal gradients in species diversity: The search for the primary cause. *Oikos* 65, 514–527.
- Rohde, K. (1997). The larger area of the tropics does not explain latitudinal gradients in species diversity. *Oikos* 79, 169–172.
- Rohde, K. (1998). Latitudinal gradients in species diversity. Area matters, but how much? *Oikos* 82, 184–190.
- Rohde, K., Heap, M., and Heap, D. (1993). Rapoport's rule does not apply to marine teleosts and cannot explain the latitudinal gradient in species richness. *Am. Nat.* 142, 1–16.
- Rosenzweig, M. L. (1995). *Species Diversity in Space and Time*. Cambridge Univ. Press, Cambridge, MA.
- Rosenzweig, M. L., and Sandlin, E. A. (1997). Species diversity and latitude: Listening to area's signal. *Oikos* 80, 172–175.
- Roy, K., Jablonski, D., and Valentine, J. W. (1994). Eastern Pacific molluscan provinces and the latitudinal diversity gradient: No evidence for "Rapoport's rule." *Proc. Natl. Acad. Sci. USA* 91, 8871–8874.
- Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *Am. Nat.* 133, 240–256.
- Stevens, G. C. (1992). The elevational gradient in altitudinal range: An extension of Rapoport's latitudinal rule to altitude. *Am. Nat.* 140, 893–911.
- Stevens, R. D., and Willig, M. R. (1999). Size assortment in New World bat communities. *J. Mammal.* 80, 644–658.
- Taylor, P. H., and Gaines, S. D. (1999). Can Rapoport's rule be rescued? Modeling causes of the latitudinal gradient in species richness. *Ecology*, 2474–2482.
- Terborgh, J. (1973). On the notion of favorableness in plant ecology. *Am. Nat.* 107, 481–501.
- Voss, R. S., and Emmons, L. H. (1996). Mammalian diversity in Neotropical lowland rainforests: A preliminary assessment. *Bull. Am. Mus. Natural History* 230, 1–115.
- 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.