LATITUDINAL GRADIENTS OF BIODIVERSITY:
Pattern, Process, Scale, and Synthesis

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■ **Abstract** The latitudinal gradient of decreasing richness from tropical to extratropical areas is ecology's longest recognized pattern. Nonetheless, notable exceptions to the general pattern exist, and it is well recognized that patterns may be dependent on characteristics of spatial scale and taxonomic hierarchy. We conducted an extensive survey of the literature and provide a synthetic assessment of the degree to which variation in patterns (positive linear, negative linear, modal, or nonsignificant) is a consequence of characteristics of scale (extent or focus) or taxon. In addition, we considered latitudinal gradients with respect to generic and familial richness, as well as species evenness and diversity. We provide a classification of the over 30 hypotheses advanced to account for the latitudinal gradient, and we discuss seven hypotheses with most promise for advancing ecological, biogeographic, and evolutionary understanding. We conclude with a forward-looking synthesis and list of fertile areas for future research.

INTRODUCTION

The oldest and one of the most fundamental patterns concerning life on earth is the increase in biological diversity from polar to equatorial regions (Brown & Lomolino 1998, Gaston 1996a, Rosenzweig 1995, Willig 2001). Indeed, a cogent statement of the gradient was articulated by von Humboldt early in the nineteenth century (Hawkins 2001). With notable exceptions, the pattern generally holds true, regardless of the biota's taxonomic affiliation (e.g., mammals, fishes, insects, and plants), geographic context (e.g., all continents and oceans), or time domain (e.g., Recent and 70 Mya). It was recognized clearly by the progenitors of evolutionary

theory (Darwin 1862, Wallace 1878), and has been integral to the thinking of some of the most influential biologists of the past century (Dobzhansky 1950, Hutchinson 1959, MacArthur 1972). Indeed, a lustful preoccupation with high tropical biodiversity stimulated the conceptual development of much of community ecology. Similarly, serious concerns about the erosion of biodiversity at global, regional, and local scales have catalyzed a considerable body of research in conservation biology (Chown & Gaston 2000).

Broad recognition of the latitudinal gradient occurred in the 1800s, with an emphasis on quantification from the 1950s onward. The number of explanatory hypotheses for the gradient proliferated at the end of the twentieth century, with few attempts to falsify them in the sense of strong inference (Platt 1964). Although, a number of synthetic reviews have set the stage for advancement (especially Rohde 1992, Schemske 2002), rigorous attention to questions of spatial scale only has begun to characterize quantitative research concerning latitudinal gradients of biodiversity. Similarly, the relative importance of causal mechanisms, including stochastic processes, remains a poorly understood yet critical area for future investigation and synthesis. Latitudinal gradients of diversity are ultimately dependent on the historical, geographic, biotic, abiotic, and stochastic forces (Schemske 2002) affecting the geometry, internal structure, and location of species ranges in ecological or evolutionary time. Indeed, latitude is a surrogate for a number of primary environmental gradients (e.g., temperature, insolation, seasonality) that interact and are correlated to each other, making direct tests of hypotheses difficult and controvertible.

Biodiversity: Context and Constraints

Biodiversity became popularized as a term to mean "life on earth" as a consequence of a "National Forum on BioDiversity" that met in Washington D.C. in September 1986. In its full amplification, biodiversity includes variation in life at a spectrum of hierarchical levels, from genes to the biosphere (Swingland 2001). Although biodiversity has genetic, taxonomic, and ecological attributes (Gaston & Spicer 1998), we focus on a taxonomic component—species richness—because that characteristic of biodiversity has been the predominant concern of most research concerning latitudinal gradients. Nonetheless, we examine latitudinal gradients in other aspects of biodiversity (e.g., generic and familial richness, species evenness and diversity), albeit in a more limited fashion, when such patterns have been quantified over broad spatial extents.

Unlike most research in biology and much in ecology, understanding patterns and mechanisms related to the latitudinal gradient is limited severely by practical and ethical concerns. The broad geographic domain of research (countries, continents, and hemispheres) means that the primary data concerning the presence and absence of species for a particular biota are likely compiled by numerous scientists over a large number of years. Moreover, powerful investigative approaches associated with experimental design and manipulation are not feasible or ethical, thereby

limiting progress in identifying the mechanistic bases of patterns. Nonetheless, a variety of statistical and simulation approaches provide considerable insight to latitudinal patterns and mechanisms that give rise to them, as they do for other macroecological patterns regarding population density, body mass, or range size (Brown 1995).

Spatial Scale

In general, considerations of spatial scale have become increasingly important in ecology because the detection of pattern and the identification of causal mechanisms critically depend on it (Gardner et al. 2001, Levin 1992, Peterson & Parker 1998). Two attributes of scale, focus and extent (sensu Scheiner et al. 2000), are particularly relevant to studies of gradients regarding species richness. The focus of a research design is defined by the inference space to which each datum applies, whereas the extent of a research design relates to the inference space to which the entire collection of data applies in an analysis. Thus, the focus is intimately associated with the size or dimensions of sampling units, whereas the extent is defined by the geographic or ecological space that has been sampled in the overall analysis. As might be expected, analyses of the latitudinal gradient in richness have involved a variety of different foci and extents (Willig 2001), making direct comparison among studies difficult. Nonetheless, the latitudinal increase in taxonomic richness toward the tropics characterizes studies with a focus on broad climatic zones (e.g., Fischer 1960), assemblages occupying arbitrary geographic subdivisions such as quadrats (e.g., Kaufman 1994, Simpson 1964, Willig & Selcer 1989, Wilson 1974) or bands (e.g., Kaufman & Willig 1998, McCoy & Connor 1980, Willig & Gannon 1997, Willig & Sandlin 1991) and local ecological communities (e.g., Kaufman 1998, Stevens & Willig 2002).

Scale dependence occurs when the form (e.g., linear versus quadratic versus modal) or parameterization (e.g., magnitude and sign of regression coefficients) of a relationship changes with focus or extent. Studies involving species richness, as well as with most other aspects of biodiversity, are expected to be strongly dependent on spatial scale because of the manner in which species richness increases with area. Larger areas contain more individuals, more habitats, and more biomes or biogeographic provinces than do smaller areas (Rosenzweig 1995). As a consequence of all three considerations, species richness increases as well. In any particular study, the exact way in which species richness increases with area determines the impact of scale on biological conclusions (Kolasa & Pickett 1991, Palmer & White 1994). A variety of models have been advanced to characterize the species-area relationship. The two most common are the exponential or semilogarithmic function of Gleason (1922, 1925) and the power function of Arrhenius (1921, 1923a,b), although alternative models based on the random placement of individuals exist as well (Coleman 1981, Coleman et al. 1982).

Regardless of the particular algorithm used to characterize the species-area relationship, three idealized kinds of scale effects (Scheiner et al. 2000,

Figure 1) are relevant to the latitudinal gradient in diversity, including scale-invariant, rank-invariant, and scale-dependent patterns. If the forms (e.g., power versus semilogarithmic function) of the species area curves differ at different latitudes, then scale dependence in the latitudinal gradient will be pervasive and difficult to control in comparative analyses. Thus, differences among studies in the form or parameterization of the latitudinal gradient could be a consequence of inherent differences among them with respect to characteristics of scale (i.e., focus or extent) or with respect to biological, historical, or geographical characteristics.

Several studies of the latitudinal gradient have attempted to control for considerations of focal scale (i.e., area) through various kinds of covariance analysis in the context of regression models (e.g., Kaufman & Willig 1998, Mares & Ojeda 1982). Most of these are problematic because of methodological concerns. Such studies have been based on focal units with linear dimensions ranging from 62.5 km to 500 km, or degree-based dimensions ranging from 1° to 10° (Anderson & Marcus 1993). Quadrats defined by meridians and parallels are of variable size because the distance encompassed by 1° of longitude depends on latitudinal position. Longitudinal meridians converge toward the poles so that the area of degree-based quadrats decreases as latitude increases, creating a systematic bias that confounds measures of area and latitude. Even quadrats based on linear dimensions differ in the amount of land they contain because most coastal quadrats will not be full of land (Rosenzweig 1995). Consequently it is difficult to disentangle areal effects from other geographic, historical, or ecological phenomena associated with land-ocean interfaces. Finally, almost all studies of latitudinal gradients fail to take into account the spatially autocorrelated nature of measures of species richness. Because species ranges are idealized as continuous surfaces, proximate sampling units are likely to have more similar magnitudes of richness than would more distant sampling units. Failure to account for autocorrelation can result in unreliable or biased estimates of significance in statistical analyses (Dale & Fortin 2002, Diniz-Filho et al. 2002a, Legendre 1993). For example, Baquero & Telleria (2001) examined patterns of species richness at 289 evenly distributed sampling points in Europe. Species richness, the number of endemic species, and the number of rare species were related negatively to latitude. Nonetheless, latitudinal effects became nonsignificant after accounting for the geographic proximity of points. Caution is needed in interpreting such results as a plethora of statistical approaches exist for dealing with autocorrelation, especially when environmental variables are correlated with spatial distances. Because latitude itself is an explicitly spatial dimension, its treatment in such analyses requires particularly careful consideration. Two general approaches seem appropriate. The first involves using subsets of the data that are sufficiently distant from each other so that autocorrelative effects are eliminated from analyses. The second involves covariance analyses for which distance effects that are independent of latitude (e.g., "pure distance," such as those associated with longitude) are distinguished from distance effects that include differences along environmental gradients that parallel meridia.

Recent studies (Lyons & Willig 2002) overcame many of these problems by examining nested quadrats of fixed area (1000, 10,000, 15,000, 20,000, and 25,000 km^2) that were centered at regular intervals in the continental New World (i.e., at 2.5° latitudinal intervals along each 5° meridian). Following the pioneering work of Pastor et al. (1996), Lyons & Willig (2002) directly evaluated if the parameterization of the power function depended on latitude. Results for both bats and marsupials in the New World documented that the slope (z) of the power function ($S = CA^z$, where S is species richness, A is quadrat area, and ln C [intercept] and z [slope] are fixed constants derived from least-squares analysis of the log-log transformation of the relationship) systematically decreased with decreased latitude. Lyons & Willig (2002) suggested that some of the very mechanisms (e.g., environmental variation, geometric constraints, Rapoport-rescue effects) thought to promote the latitudinal gradient in richness would also predispose those patterns to be scale sensitive.

SPATIAL DYNAMICS OF DIVERSITY

The richness of any region is a consequence of two factors: the richness of each of the smaller areas that compose it, and the turnover in species composition among them (Whittaker 1960). A variety of terms has been suggested for these three levels of diversity, depending on their spatial scale and ecological characteristics (Whittaker 1977), but their use has not been consistent (Koleff & Gaston 2002). Schneider (2001) provided a reasonable summary of terminology that is of relevance to the latitudinal gradient. Diversity can be characterized at various focal scales including point diversity (richness of a subset of a community), alpha diversity (richness within the full extent of a single community), gamma diversity (richness of a landscape that comprises different communities), and epsilon diversity (richness of a broad geographic area that comprises different landscapes). Although reasonable, these are arbitrary distinctions along a continuum of possible focal scales. In practice, it is difficult to distinguish between gamma and epsilon diversity in a biogeographic context because the boundaries of and distinction between a landscape and a broad region are unclear. Consequently, we distinguish among three focal scales: point diversity, alpha diversity, and gamma diversity (here meaning the richness of an area comprising multiple communities). Three other measures of diversity refer to turnover among focal units (Schneider 2001): local beta diversity (change in species composition among subsets of a community), beta diversity (change in species composition among different communities in a landscape or along an environmental gradient), delta diversity (change in species composition along a climate gradient or among geographic areas). Latitude is clearly a geographic gradient that includes multiple communities, reflecting climatic and environmental characteristics. Again, the distinction between kinds of turnover in a biogeographic context is arbitrary, and we adopt the more popular term, beta diversity, to mean turnover among focal units representing distinct communities.

Beta diversity can be quantified in several interrelated ways. One approach is designed so that the product of beta diversity and alpha diversity equals gamma diversity (Harrison et al. 1992; Whittaker 1960, 1972). An alternative formulation has been constructed so that the sum of alpha and beta diversities yields gamma diversity (e.g., Williams 1996). The additive metric recently has been the focus of a cogent review (Veech et al. 2002), and shows much promise for its application to issues in conservation biology (Gering et al. 2003). Another type of beta diversity is based on consideration of species losses and gains along a gradient or transect (Wilson & Shmida 1984). The selection of a particular index depends on characteristics of the focal samples, the domain or gradients over which they are evaluated, and the hypotheses of interest.

A large body of evidence (see Empirical Patterns, below) (Figure 2) supports an inverse relationship between gamma diversity and latitude. This could be a consequence of underlying gradients in alpha diversity, beta diversity, or both. Beta diversity increases from poles to tropical areas in a number of groups: mammals (Kaufman 1998, Stevens & Willig 2002), birds (Blackburn & Gaston 1996b, Koleff & Gaston 2001), shallow water bryozoans (Clarke & Lidgard 2000), trees (D.F. Sax, unpublished data), and herbaceous plants (Perelman et al. 2001). Moreover, the proportion of the regional biota represented in local communities was equivalent in North American trees and South American herbs, after controlling for hemisphere (Perelman et al. 2001; D.F. Sax, unpublished data). For mammals in the New World, Kaufman (1998) corroborated the poleward decrease in beta diversity but detected a plateau effect in tropical areas, suggesting nonlinearities in the gradient.

At least three studies simultaneously have analyzed latitudinal variation in alpha, beta, and gamma diversity, providing synoptic assessments of latitudinal gradients. Nonetheless, the spatial limits associated with measures of alpha and gamma diversity remain somewhat subjective, albeit informed by the expert opinion of the taxonomic specialists in each study. That is, the spatial limits of a bat community may be larger than those of a rodent community, both of which are considerably larger than those of a community of microarthropods. This transpires because of the different grains at which these taxa likely perceive their environment. For nonvolant species of mammals in North America, latitudinal patterns differed among levels of diversity (Kaufman 1998). Alpha diversity was relatively constant across the Temperate Zone but increased into the tropics, with nearly twice as many species in tropical communities as were found in temperate communities.

Figure 2 A broad survey of the published literature (see text for details) illustrates the complexion (*A*, tempo of publication; *B*, taxonomic focus of research; *C*, geographic focus of research) and scale (*D*, geographic extents of analysis; *E*, geographic characteristics) of research on the latitudinal gradient of richness. The conclusion of most studies (*F*) was that the relationship between richness and latitude was negative, although positive, modal, and no patterns were detected as well.
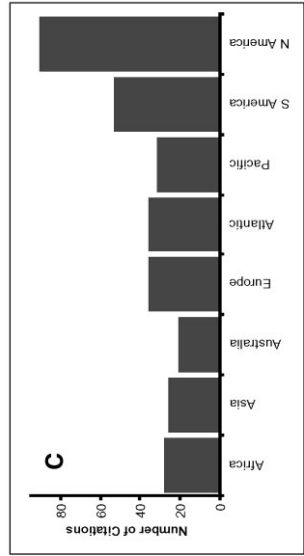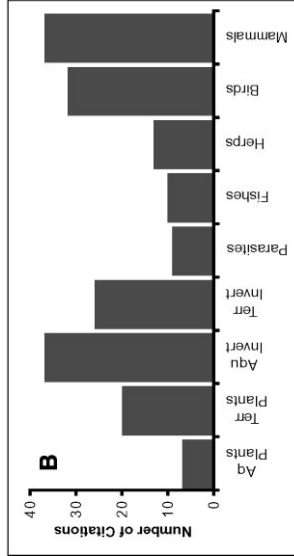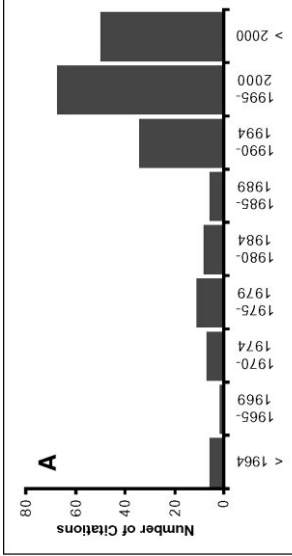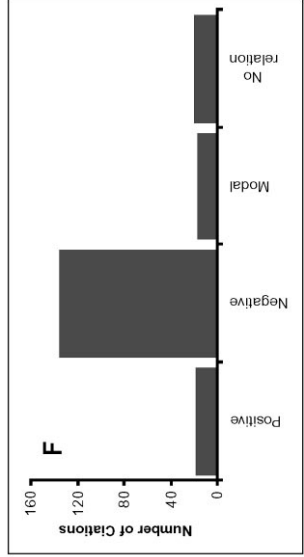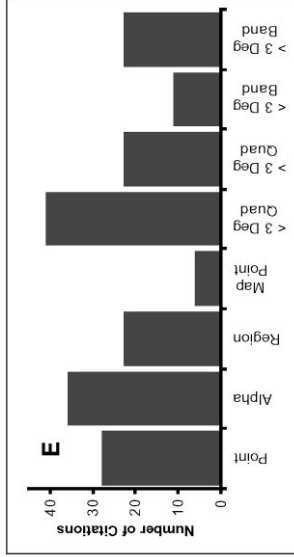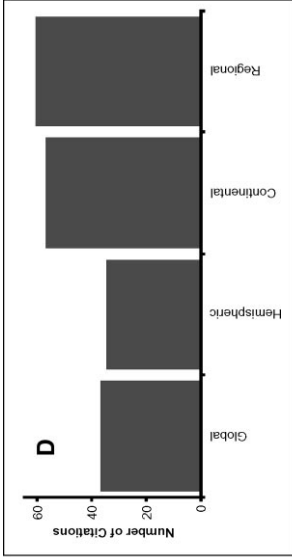
In contrast, gamma and beta diversity increased steadily with decreasing latitude throughout the Temperate Zone, but the rate of increase decreased within the tropics (i.e., gamma diversity exhibited a negative sigmoidal relationship). Beta diversity remained more or less constant (i.e., attained a plateau) below 30° N (Kaufman 1998). Stevens & Willig (2002) demonstrated linear relationships between latitude and all three levels of diversity for New World bats. A positive association existed between alpha and gamma diversity. Moreover, the rate of increase in gamma diversity toward the tropics was higher than that for alpha diversity, with both measures approximately equal at the highest latitudes and diverging in magnitude toward the equator. Thus, alpha diversity plays a more dominant role in shaping gamma diversity in extratropical areas, whereas beta diversity plays a more dominant role in shaping gamma diversity in tropical areas in this taxon. In contrast, shallow-water bryozoans in the northern Atlantic Ocean show no evidence of a latitudinal gradient in alpha diversity (Clarke & Lidgard 2000). Moreover, beta and gamma diversity decreased with increased latitude. In conclusion, patterns of alpha, beta, and gamma diversity differed among studies, but the way in which beta diversity interacted with alpha diversity to produce latitudinal gradients in gamma diversity was consistent.

A deep understanding of latitudinal gradients is predicated on simultaneous quantification of gradients for all three levels of diversity. From a methodological perspective, a unified framework is needed to relate patterns based on different measures of beta diversity. This is especially critical because turnover that is measured at different scales often is based on different indexes of beta diversity, and the detection and strength of latitudinal gradients of beta diversity are clearly scale dependent (Arita & Rodriguez 2002, Koleff & Gaston 2002). Until the differences that are due to scale can be distinguished from those related to choice of metric for estimating turnover, it will be difficult to assess the qualitative generality of any latitudinal pattern of beta diversity, much less its association with alpha and gamma diversity.

EMPIRICAL PATTERNS: SPECIES RICHNESS

To obtain information with which to characterize latitudinal gradients in extant species richness, we conducted a suite of literature searches. Our primary endeavor utilized SciSearch, the Science Citation Index Citation Database located on the Institute for Scientific Information website (http://webofscience.com/ciw.cgi). We searched for the key-word combinations "latitud* and diversity and gradient*," "latitud* and diversity and species," "latitud* and richness and gradient*," "latitud* and richness and species," "gradient* and diversity and species," as well as "gradient* and richness and species" up to the end of 2002. The asterisk (*) is a wildcard of undetermined length. By using this wildcard, one can search for a basic root word with different endings. In a second search, we used a variety of search engines including Agricola, ArticleFirst, Biosys, Biological and Agricultural Index, Cambridge Scientific Abstracts, and JSTOR to find additional

citations up to 2001. We used the search phrases "diversity and latitude," "richness and latitude," "latitudinal gradient," "diversity gradient," and "richness gradient." Additional journal articles were encountered by perusing the bibliographies of articles on latitudinal gradients in diversity that were identified by this suite of searches.

The publications discovered through this process (N = 162) were perused, categorized, and tallied according to focal scale and latitudinal extent, as well as by the detected latitudinal pattern of species richness. When a single article presented analyses for a number of taxa (e.g., mammals, birds, herptiles) or at a number of scales (e.g., alpha and gamma diversity), results for each combination of analysis were tallied individually [i.e., the number of analyses (191) > the number of articles (162)].

The popularity of the latitudinal gradient as a research topic has grown rapidly over the past 40 years (Figure 2*A*). Moreover, latitudinal patterns have been examined rather thoroughly across taxa, but with a disproportionate emphasis on aquatic invertebrates, birds, and mammals (Figure 2*B*). Similarly, the gradient has been examined broadly from a geographic perspective, covering most continents and a number of oceans (Figure 2*C*). From a methodological perspective, the gradient has been examined at a variety of spatial scales with respect to aspects of extent (Figure 2*D*) and focus (Figure 2*E*). The majority of analyses (135, approximately 71%) have corroborated that the latitudinal gradient is one in which species richness increases toward the tropics (Figure 2*F*). Patterns in which species richness peaked at mid-latitudes or decreased toward the tropics were far less common, only as prevalent as was no relationship at all.

Evidence Corroborating the Classical Pattern

The negative association between taxonomic richness and latitude (i.e., the classical pattern) has been demonstrated for latitudinal extents that are short (i.e., <20° latitude: Cushman et al. 1993, Gotelli & Ellison 2002, Meserve et al. 1991) and long (i.e., ≥20° latitude; Fischer 1960, Rosenzweig 1992), as well as when estimated as point (Gentry 1988, Kocher & Williams 2000, Rex et al. 1993), alpha (Barbour & Brown 1974, Meserve et al. 1991, Stevens & Willig 2002), or gamma diversity (Anderson 1977, Ellison 2002, Gaston 2000). Moreover, this pattern has been described for many major organismal groups including: terrestrial plants (Cowling & Samways 1995, Gentry 1988), mangrove trees (Ellison 2002), marine protists (Culver & Buzas 2000), coral (Harriot & Banks 2002, Reyes-Bonilla & Cruz-Pinon 2000), mollusks (Rex et al. 1993; Roy et al. 1994, 1996, 1998; Stehli et al. 1967; Taylor & Taylor 1977), marine and freshwater arthropods (Dworschak 2000, Steele 1988), terrestrial arthropods (Cushman et al. 1993, Davidowitz & Rosenzweig 1998, Kocher & Williams 2000, Lobo 2000), marine and freshwater fishes (Barbour & Brown 1974, Oberdorff et al. 1995, Stevens 1996), herptiles (Currie 1991, Kiester 1971, Schall & Pianka 1978), birds (Blackburn & Gaston 1996a, 1996b, 1997; Cardillo 2002; Cook 1969; Diniz-Filho et al. 2002b; Rahbek

& Graves 2001), and mammals (Kaufman 1995, Lyons & Willig 2002, McCoy & Connor 1980, Simpson 1964). Although Platnick (1991) warned that global views about patterns of biodiversity may be subject to a "megafauna bias," it is clear that the classical pattern is a pervasive characteristic of life on earth, especially when the gradient comprises broad spatial scales (Figure 3).

Some of the best examples of the classical pattern have been based on the gamma diversity of mammals, especially in the New World (Figure 4), but also in Africa. In North America, the classical pattern has been corroborated by a multitude of investigators (Anderson 1977, Badgley & Fox 2000, Currie 1991, Davidowitz & Rosenzweig 1998, McCoy & Connor 1980, Pagel et al. 1991, Rosenzweig 1992, Simpson 1964, Wilson 1974). Compared with terrestrial mammals, bats exhibited steeper latitudinal gradients in North America and disproportionately contributed to the tropical increase in species richness of mammals in general (Kaufman 1995; Ruggiero 1994, 1999). In the past decade, the geographic extent of latitudinal studies of New World mammals have expanded to jointly consider North and South America (e.g., Kaufman 1995, Kaufman & Willig 1998, Lyons & Willig 2002, Willig & Gannon 1997, Willig & Sandlin 1991, Willig & Selcer 1989). Although spatial-scale dependence characterized the relationship for bats and marsupials (Lyons & Willig 2002) in the Western Hemisphere, the Mammalia exhibited indistinguishable latitudinal gradients in North and South America once accounting for differences in area of 2.5° and 5° latitudinal bands (Kaufman & Willig 1998). The classical pattern has been demonstrated in Africa as well (Andrews & O'Brien 2000, Cowlishaw & Hacker 1997, Eeley & Foley 1999).

The form of the latitudinal gradient in gamma diversity in the New World differs among mammalian orders (Kaufman 1995, Ruggiero 1994), with maxima in richness occurring at different locations for different taxa. Nonetheless, peaks of species richness for all orders occurred within 30° of the equator, except for the Insectivora, which attained maximum richness in the Temperate Zone of North America. The rate of increase in species richness toward the tropics was steepest for bats and primates compared with other mammalian orders.

Most of the work on latitudinal gradients of bird species richness also has been conducted in the New World. In general, species richness increased toward the equator (Anderson 1984; Blackburn & Gaston 1996a, 1997; Buckton & Ormerod 2002; Cardillo 2002; Cook 1969; Currie 1991; Diniz-Filho et al. 2002b; Gaston 2000; Rabinovich & Rapoport 1975; Rahbek & Graves 2001; Schall & Pianka 1978; Tramer 1974). Although methodological differences existed among studies, especially regarding the inclusion or exclusion of wintering ranges in the determination of species richness, results were correlated (Blackburn & Gaston 1996a, 1996b, 1997) or similar (Tramer 1974).

Latitudinal gradients of species richness for fishes generally corroborated the current paradigm. The tropical increase in richness was true for marine and freshwater taxa as well as for assemblages in lentic and lotic habitats. Although most highly correlated with the surface area of lakes, the species richness of fishes

increased with decreased latitude throughout the world (Barbour & Brown 1974). Similarly, the species richness of fish assemblages from 292 rivers throughout the world increased toward the tropics (Oberdorff et al. 1995). For global extents, the number of species of pelagic fishes was lowest at high latitudes and highest at low latitudes, with maximum species richness at approximately 15° N (Rohde 1978a). In addition, fish species richness increased toward the equator in the Atlantic Ocean (Angel 1993, Macpherson 2002, McClatchie et al. 1997), Pacific Ocean (Stevens 1996), and Sea of Japan (Kafanov et al. 2000). Moreover, significant latitudinal gradients were obtained for taxonomic subsets of the fish fauna. For example, species richness of both teleosts and elasmobranch fishes increased toward the equator (Macpherson & Duarte 1994).

Latitudinal gradients in the Mollusca are well established (Crame 2000, 2002; Rex et al. 1993; Roy et al. 1994, 1996, 1998; Stehli et al. 1967). Latitude accounts for significant amounts of variation in the number of species, genera, and families, as well as in the number of species within functional groups, in benthic marine gastropods and bivalves from the eastern Pacific (Roy et al. 1994, 1996, 1998, 2000). Moreover, patterns of generic and familial richness are correlated highly with those of species richness (Roy et al. 1996). For all three levels in the taxonomic hierarchy, richness increased toward the tropics in equivalent fashions. Stehli et al. (1967) reported similar results regarding the species, generic, and familial patterns of taxonomic diversity in Recent bivalves.

Predatory gastropods on the eastern Atlantic Shelf exhibited a latitudinal gradient in which the number of species decreased toward the poles (Taylor & Taylor 1977). Roy et al. (1998) documented a similar gradient in the species richness of prosobranch gastropods. They collected data regarding the geographic ranges of 3916 species from throughout the western Atlantic and eastern Pacific. Gradients of richness were similar in the two oceans despite their marked physical and historical differences. Nonetheless, differences appeared in the comparison of patterns in Northern and Southern Hemispheres. More specifically, latitudinal gradients were significant and steep in the Northern Hemisphere, based on local samples of deep-sea bivalves, gastropods, and isopods, but less strong in the Southern Hemisphere as a result of appreciable interregional variation (Rex et al. 1993). Moreover, younger clades within the Bivalvia exhibited the steepest gradients in richness (Crame 2000).

Exceptions to the Classical Pattern

A number of exceptions exist regarding the strength and direction of latitudinal gradients in richness. In a small proportion of cases (Figure 3), the relationship between species richness and latitude was nonsignificant (10%; e.g., Bolton 1994, Clarke & Lidgard 2000, Dexter 1992, Dingle et al. 2000, Ellingsen & Gray 2002, Mann et al. 1999, Oliva 1999, Reid 1994, Poulin 1995, Poulsen & Krabbe 1997, Pysek 1998, Rohde 1999), modal (9%; e.g., Chown et al. 1998, Davidowitz & Rosenzweig 1998, France 1992, Janzen 1981, Krystufek & Griffiths 2002, Price

et al. 1998, Skillen et al. 2000), or positive (10%; e.g., Blaylock et al. 1998, Hawkins & Compton 1992, Heip et al. 1992, Heip & Craeymeersch 1995, Lambshead et al. 2000, Rabenold 1979, Santelices & Meneses 2000). Exceptions primarily were associated with (*a*) narrow latitudinal extents (i.e., a form of scale dependence), (*b*) species with parasitic life histories, or (*c*) aquatic floras.

Many of the exceptions to the classical pattern (36%) were associated with scale and occurred when the gradient in richness was quantified over short latitudinal extents ($<20°$ latitude). Indeed, analyses based on small latitudinal extents had a significantly greater proportion of results that failed to corroborate the classical pattern (Contingency Analysis—$G = 9.39$, d.f. $= 1$, $P = 0.002$). The number of positive or nonsignificant patterns was quite low (Figure 3) when the extent of the analyses was broad ($\geq 20°$ latitude), with examples scattered among the various organismal groups. In contrast, half of the analyses based on narrow latitudinal extents failed to corroborate the classical pattern. Variation and heterogeneity associated with more local geography, geology, hydrology, or history likely overpowered the effects of causative mechanisms associated with latitude in such cases.

The earliest described exceptions to classical latitudinal pattern involved the Hymenoptera, in particular wasps, and especially members of the parasitoidal Ichneumonidae (Janzen 1981, Price et al. 1998, Skillen et al. 2000). In North America, species richness of ichneumonids peaked at $38°$–$42°$ N (Janzen 1981), although some have suggested a broader peak (Skillen et al. 2000). The mechanistic basis of this mid-latitudinal peak in richness remains uncertain, although mid-latitudinal peaks in host density (Janzen 1981) and mid-domain effects (Skillen et al. 2000) have been suggested to be important.

The species richnesses of ecto- and endoparasites do not respond to latitude in a consistent fashion (Blaylock et al. 1998, Poulin 1999, Rohde 1978b). In general, the number of ectoparasites in fish, birds, or mammals was unrelated to latitudinal variation (Poulin 1995). Similarly, the species richness of gastrointestinal helminths of teleost fish did not change in a consistent fashion with latitude (Rohde 1998). Moreover, no significant latitudinal variation existed in the number of species of trematodes parasitizing fish (Rohde 1999) or in the number of species of metazoan parasites found on jack mackerel (Oliva 1999). Symbiotic associations, especially for endoparasites of homeotherms, insulate species from the environmental conditions faced by their hosts, thereby mitigating any latitudinal mechanisms that might influence the species richness of parasites. Nonetheless, even modest host specificity coupled with a latitudinal gradient in host species richness would be expected to effect the classical pattern in parasites as well.

With few exceptions (Pielou 1977, Santelices & Meneses 2000), aquatic plants do not exhibit latitudinal gradients. Bolton (1994) investigated the distribution and abundance of seaweeds from 29 floras throughout the world. Although subtropical and tropical areas exhibited the highest levels of species richness, they also exhibited relatively low levels. No consistent latitudinal trend in species richness was detected, and the highest number of species did not occur in floras situated nearest to the equator. Crow (1993) corroborated this finding for aquatic angiosperms

from throughout North and Central America. More specifically, higher levels of angiosperm richness existed at warm temperate sites than at tropical sites. Similarly, a tropical peak in richness was absent for North American charophytes (Mann et al. 1999). Latitude is also unimportant in determining the number of aquatic macrophytes in Fennoscandia (Virola et al. 2001). The reasons remain enigmatic.

Finally, secondary marine birds and mammals (i.e., taxa that have reverted to a marine lifestyle after diverging from terrestrial ancestors) exhibited extratropical peaks in species richness. These taxa include pelagic birds and members of the mammalian suborder Pinnipedia (Chown et al. 1998, Proches 2001). The modal patterns of species richness of secondary marine organisms may be related to an increase in heterogeneity and resources that occurs in association with the Subtropical Convergence and Antarctic Polar Frontal Zone.

EMPIRICAL PATTERNS: SPECIES DIVERSITY AND EVENNESS

Two critical considerations apply when comparing studies of latitudinal gradients between local and regional levels. Although richness at the local and the regional scale is interdependent (Ricklefs & Schluter 1993), these scales represent distinct levels of biological organization (i.e., reflecting ecological mechanisms that operate within communities versus those ecological and historical mechanisms that effect turnover among communities in a region). Accordingly, the importance of particular structuring mechanisms likely differs between such levels of organization. Mechanisms such as interspecific interactions or dispersal limitations are likely more important at the local level, whereas mechanisms related to speciation and extinction are more important at the regional level (Ricklefs & Schluter 1993). Moreover, species abundances can be quantified more readily at the level of local communities than at larger spatial scales. This facilitates consideration of weighted measures of diversity such as species evenness, species dominance, or species diversity. Such measures provide for more comprehensive examinations of latitudinal gradients. Drawbacks to such approaches include the rarity of density data for multiple communities as well as a tendency for such studies to encompass relatively narrow latitudinal gradients when the data do exist.

Porembski et al. (1996) evaluated patterns in the local diversity of inselbergs (i.e., steep ridges or hills that remain after a mountain erodes within an otherwise flat terrain) along a 6° latitudinal transect in the Ivory Coast of Africa. No relationship existed between the number of plant species and latitude. Nonetheless, dominance (Simpson index) was related to latitude and increased from north to south (Porembski et al. 1995). Bowman (1996) investigated the diversity of plant communities along a latitudinal gradient in northern Australia. Although beta diversity among equal-sized quadrats within each of 15 cells increased toward the tropics, species richness and Shannon's diversity exhibited no significant latitudinal gradient.

Marine invertebrates exhibited a variety of different latitudinal gradients with respect to species richness, evenness, and diversity. Rex et al. (2000) found that the number of species of bivalves, gastropods, and isopods as well as species evenness (Pielou's index) and diversity (Shannon's index) in both the Northern and Southern Hemisphere decreased toward the poles. For copepods of the Atlantic Ocean, average evenness was greater and variance of evenness lower at the equator than at higher latitudes (Woodd-Walker et al. 2002). In contrast, Errhif et al. (1997) detected no significant latitudinal relationships for copepods with respect to Shannon's diversity or Shannon's evenness along a transect that spanned 23° of latitude in the Antarctic Ocean.

The richness and evenness of species of wireworms (Collembola: Elateridae) exhibited opposite latitudinal gradients in Central Russia (Penev 1992). More specifically, species richness decreased and evenness increased with increased latitude. Their interaction caused species diversity to exhibit no significant change with latitude.

Vertebrates also exhibited inconsistent latitudinal patterns of taxonomic diversity. The species richness, diversity, and evenness of demersal fishes exhibited positive relationships with latitude in the southern Atlantic Ocean in the vicinity of New Zealand (McClatchie et al. 1997). The species richness and diversity of Finnish birds of prey exhibited positive associations with latitude (Solenon 1994). For waders in Fennoscandia, the latitudinal relationship was positive for species richness, negative for species evenness, and nonsignificant for species diversity (Jarvinen & Vaisanen 1978). Similarly, no significant relationship existed between latitude and species richness, evenness, and diversity of small mammal communities on clearcuts in Sweden between 55° and 65° N (Hansson 1992). In contrast, small mammal communities in North America did exhibit latitudinal relationships in evenness (negative) and dominance (positive), as characterized by rank-abundance relationships (Kaufman 1998). Finally, on the Iberian Peninsula, small mammal diversity (Shannon's index) determined from barn owl pellets increased with increased latitude (Barbosa & Benzal 1996). Although such positive relationships between aspects of mammalian biodiversity and latitude were uncommon, this particular result may have been associated with increased habitat complexity from north to south in this region of Europe.

Although patterns of species evenness and richness can be similar, they may describe two unique aspects of spatial variation among communities (see review by Stirling & Wilsey 2001). Moreover, if communities or assemblages become richer as a consequence of sustaining more rare species, then latitudinal increases in richness should be accompanied by latitudinal decreases in evenness. Stevens & Willig (2002) evaluated the spatial variation of 32 New World bat communities based on 14 different measures of taxonomic diversity including those that were sensitive to changes in richness, evenness, diversity, and dominance. A factor analysis determined that the spatial variation in aspects of richness was independent of spatial variation in aspects of evenness. In fact, the species richness of New World bat communities exhibited significant and strong latitudinal gradients,

whereas evenness exhibited no relationship with latitude. Equally important, no two measures of richness, evenness, dominance, or diversity varied spatially in identical fashions. This cautions that comparisons of aspects of biodiversity that are weighted by species abundances may be compromised if they are not based on identical indexes. Moreover, it clearly demonstrates that all measures of diversity do not vary in concert along latitudinal gradients.

EMPIRICAL PATTERNS: ANCIENT ASSEMBLAGES AND HIGHER TAXA

The latitudinal gradient has been demonstrated in contemporary time for a spectrum of taxa across the globe because individual organisms can be observed, identified, and counted at a variety of spatial and temporal scales. A number of methodological issues concerning the assessment of large-scale patterns of diversity characterize studies of extant taxa; however, quantification of latitudinal patterns in the fossil record has additional constraints that constitute a methodological challenge of Herculean dimension. Nonetheless, study of the fossil record reveals that the latitudinal gradient of richness has existed for at least a quarter of a billion years!

Biases in the fossil record have been the subject of much paleontological research (Kidwell & Holland 2002). Preservation potential differences among organisms and fossil samples are biased representations of the communities that existed in the past. These biases may be related to morphology (i.e., only species with skeletons or hard parts are preserved; soft-bodied organisms are preserved only under exceptional circumstances; Briggs & Kear 1993), mineralogy (e.g., phosphatic, aragonitic, or calcitic shells have different preservation potentials; Cherns & Wright 2000), size (i.e., larger fossils are more durable over time and are easier for paleontologists to discover; Kidwell & Holland 2002), habitat (i.e., preservation of marine organisms is more likely than preservation of freshwater or terrestrial organisms; Kidwell & Holland 2002), population size (i.e., common organisms have a higher likelihood of preservation; Kidwell & Holland 2002), and the uneven spatial and temporal distribution of rock (e.g., the absence of appropriately aged rock associated during each mass extinction event; Peters & Foote 2001). Because of these constraints, data relevant to paleolatitudinal gradients are fewer and more scattered than are those for contemporary latitudinal gradients. Nonetheless, evidence from a large span of paleontological times (from deep to shallow) has been used to construct the latitudinal gradient for two major groups: marine invertebrates and terrestrial plants.

Paleolatitudinal gradients of increasing richness toward the tropics are known from three major eras of earth history (i.e., Paleozoic, Mesozoic, and Cenozoic). Currently, the oldest evidence comes from the oceans, in the form of Permian fossils of marine brachiopods that lived 270 Mya in the Northern Hemisphere (7° N–78° N; Stehli et al. 1969). Various marine organisms provide a glimpse

of the paleolatitudinal gradient of richness at a variety of different time periods. Jurassic marine bivalves from 150 Ma (sampled over $\leq$6 Ma) exhibited a paleolatitudinal gradient of richness at specific, generic, and familial levels in both Northern and Southern Hemispheres (33° N–71° N and 30° S–75° S; Crame 2002). Stehli et al. (1969) also documented the paleolatitudinal pattern in Cretaceous planktonic Foraminifera from 70 to 80 Ma in the Northern Hemisphere (10° N–57° N). Finally, Oligocene Foraminifera from the ocean displayed a paleolatitudinal gradient in richness, which began about 35 Ma in the Pacific Ocean (0°–18° N compared with 64° S–65° S; Thomas & Gooday 1996).

The oldest documented terrestrial gradient—one pertaining to vascular plants—originated more than 100 Ma. Terrestrial angiosperms, primarily from Europe and North America, exhibited a latitudinal pattern in richness at a variety of levels in the taxonomic hierarchy for a large portion of the Cretaceous (110 Ma to 65 Ma, in ∼5 Ma time bins), with the gradient growing stronger through time (80° N–20° S; Crane & Lidgard 1989). Fossil pollen samples have been used to assess in detail the paleolatitudinal gradient of richness for angiosperms from the end of the Pleistocene through the Holocene to the present. European plant samples evinced a well-defined gradient at 1000-year intervals, from 13,000 onward to 1000 years ago. This included taxonomic richness, primarily at the specific or generic level for woody plants (Silvertown 1985), and familial richness for angiosperms (Haskell 2001). The gradient for woody plants became steeper over time, whereas the gradient for angiosperms was more consistent temporally. In addition, North American plants exhibited a latitudinal gradient in which richness of angiosperm families and woody plant genera increased toward the tropics for time periods from 12,000 or 13,000 years ago, respectively, growing steeper through time, until about 10,000 years ago, at which time the slope became constant (D.M. Kaufman & J.W. Williams, unpublished manuscript).

In summary, a latitudinal gradient in richness has existed for a considerable segment of geologic time, at numerous time steps from 270 Ma to now, and in six periods from the past three eras. Many of the ancient patterns were based on superspecific taxonomic levels, because much of the fossil data, such as those related to pollen or calcareous shells, cannot be resolved to the species level. Higher taxa have been used in numerous studies of latitudinal richness gradients for additional reasons. First, extremely broad geographic coverage of taxon-rich biotas make species-level collection of data impractical. Second, studies based on higher taxa facilitate ecological or evolutionary comparisons across diverse clades or comparisons to species-level patterns.

Gaston et al. (1995) examined familial richness of extant vertebrates, invertebrates, and plants in the same global domain. Strong latitudinal gradients were demonstrated for mammals, reptiles, amphibians, and angiosperms. In contrast, familial richness of beetles showed no relationship to latitude. In addition, latitudinal gradients of plant genera have been demonstrated consistently for North America (Qian 1998; D.M. Kaufman & J.W. Williams, unpublished manuscript). In terms of marine organisms, latitude was related inversely to richness for copepod genera,

families, and superfamilies (Atlantic Ocean: Woodd-Walker et al. 2002) as well as for coral genera (Great Barrier Reef: Fischer 1960; western Pacific and Atlantic Oceans: Stehli & Wells 1971).

In an early study, Fischer (1960) showed a latitudinal gradient in specific and generic richness for extant marine tunicates. A latitudinal gradient of generic richness was demonstrated across the globe for extant mammals as well (Gaston et al. 1995). A strong latitudinal gradient in richness existed at specific, generic, familial, and ordinal levels for North and South America, whether considered separately or as a single domain (Kaufman 1994, 1995). Nevertheless, the form of the richness-latitude relationship differed among levels in the taxonomic hierarchy—it was a negative sigmoidal model for specific and generic richness, but linear for familial and ordinal richness (Kaufman 1994, 1995). A recent study of sub-Saharan Africa demonstrated that generic richness is a good predictor of plant species richness, but familial or higher richness is a less suitable indicator (La Ferla et al. 2002). Although patterns based on higher taxa may recapitulate those at the species level, caution must be taken in assuming such a quantitative relationship.

MECHANISTIC BASES OF LATITUDINAL GRADIENTS

As early as 1807, von Humboldt provided the first hypothesis (based on climate) to explain latitudinal gradients of richness (Hawkins 2001). It embodied a general mechanism that was not specific to a particular taxon or to a particular place. In this vein, subsequent authors sought general and pervasive mechanisms that would effect a latitudinal gradient in species richness based on the premise that a single mechanism would be responsible for a pattern that is taxonomically, geographically, and temporally prevalent (Pianka 1966, but see Gaston 2000). Nonetheless, consensus about the identity of "the" mechanism has been elusive, and more synthetic multifactor approaches are emerging.

Quantitative examination of the latitudinal pattern of species richness began in the 1950s, with concurrent speculation as to its possible causes (e.g., Dobzhansky 1950, Hutchinson 1959). Pianka (1966) was the first to provide a comprehensive review of the hypotheses proposed to account for the latitudinal gradient (Table 1), including climatic stability, competition, predation, productivity, spatial heterogeneity, and time hypotheses. In the decades that followed, particular hypotheses were modified and amplified, but efforts to distinguish among them have been few. Ironically, the list of potential mechanisms has grown dramatically, so that by the 1980s, the number of explanatory hypotheses increased to ten (Brown 1988, Brown & Gibson 1983). By the early 1990s, a further threefold increase had occurred (Rohde 1992).

Hypothesized Mechanisms

A review of the potential explanatory power of each of the more than 30 currently posed hypotheses (Table 1) as a cause for the latitudinal gradient is a daunting

TABLE 1   Hypotheses proposed to account for the latitudinal gradient of diversity[*]

[†]**Abiotic-biotic**[1]	[§]**Geographic area**[RI]	[§]**Rapoport rescue**[4]
[§]**Ambient energy**[R]	[§]**Geometric constraints**[3]	Rapoport's rule[RI]
Environmental predictability[RI]	Interspecific interactions[B]	[†]**Scale hierarchy**[5]
Environmental stability[P, RI]	Competition[P, RC]	**Spatial heterogeneity**[P, B]
Harshness[B, RC]	[‡]Host diversity[RC]	Biotic spatial heterogeneity[RC]
Seasonality[RI]	Mutualism[RC]	Epiphyte load[RC]
[†]**Energetic-equivalents**[2]	Niche width[B, RC]	Number of habitats[RI]
Evolutionary rates	Predation[P, RC]	Patchiness[RC]
Extinction rate[B]	**Population dynamics**	Physical heterogeneity[RI]
Origination rate[B]	Epidemics[RC]	[‡]Solar angle[RI]
[§]**Evolutionary speed**[R]	Population growth rate[RC]	**Time**[P, B]
Temperature-dependent	Population size[RC]	Abiotic rarefaction[RI]
chemical reactions[R]	[§]**Productivity**[P, B, RI]	Ecological time[R]
	[‡]Aridity[RI]	Evolutionary time[R]

[*]Augmented from Rohde (1992) and modified from D.M. Kaufman & J.H. Brown (in review). Originating authors follow for those hypotheses not included in Rohde; for others, see Rohde (1992).

[†]Recent hypotheses not yet evaluated thoroughly in the literature; published sources are indicated by numeric superscript: ([1]Kaufman 1995, 1998; [2]Allen et al. 2002; [3]Colwell & Hurtt 1994, Lyons & Willig 1997; and [5]Whittaker et al. 2001).

[§]Hypotheses discussed in detail in text ([4]Taylor & Gaines 1999).

[‡]Hypotheses too specific to provide a general mechanism.

[P]Hypotheses included by Pianka (1966).

[B]Hypotheses included by Brown (1988, Brown & Gibson 1983).

[R]Hypotheses included by Rohde (1992; with [C] denoting "circular" hypotheses and [I] for "insufficiently supported" hypotheses).

challenge. Some hypotheses (e.g., aridity, host diversity, solar angle; Table 1) are too specific to explain the ubiquity of the latitudinal gradient. Others are circular and cannot generate the latitudinal gradient in isolation (Rohde 1992). Many are tightly interlinked because of their mechanistic bases. Previous authors (e.g., Schemske 2002) have attempted to narrow the potential mechanisms by sorting hypotheses via contrasting bases (i.e., historical or equilibrial, physical or biotic, evolutionary or ecological). Rohde (1992) offered yet another categorization, perhaps more pragmatic, in his division of hypotheses into two categories: insufficiently supported (those in which the invoked factor has not been shown to vary monotonically with latitude or richness) and circular (those that require latitudinal variation in factors extrinsic to the hypothesis) hypotheses (Table 1). This classification has practical utility as we seek to disentangle the plausibility of and evidence for potential mechanisms. For ease of consideration, rather than examine each hypothesis individually among which there are substantial redundancies, we organized them into five broad categories or themes. Each theme includes hypotheses that are related by similar mechanistic bases or by shared organizational concepts (Table 1). Importantly, many of these themes contain specific hypotheses that have little empirical support, are difficult to test, or could only

be secondary explanations for the latitudinal gradient in richness. Nonetheless, the mechanisms that are subsumed by these themes might modify empirical gradients in a substantive manner.

The time theme assumes that older communities are more diverse (Pianka 1966). Ecological forms of this hypothesis involve ecological disturbance and local dispersal (including abiotic rarefaction; Rohde 1992), whereas evolutionary forms entail geological perturbation and speciation or extinction. These hypotheses cannot be tested directly, but Pleistocene glaciations have been used to explain the relative impoverishment of the Temperate Zone as compared with the relative constancy of the tropics and its greater richness (Brown 1988).

The spatial heterogeneity theme assumes an inverse relationship between latitude and environmental complexity (Pianka 1966). Nonetheless, no general gradient in heterogeneity has been demonstrated (Rohde 1992), and any explanation based on biotic heterogeneity would require another underlying mechanism to produce that biotic gradient. Heterogeneity may be an important component of the latitudinal gradient when viewed as an axis of variation along which other factors, such as interspecific interactions, operate to mold patterns of species richness.

The interspecific interaction theme assumes that increased intensity of competition, predation, or mutualism facilitates greater species richness in the tropics. For example, competition may lead to more species per unit habitat space, or predation may reduce prey population levels, thereby allowing more prey species to coexist in the tropics (Pianka 1966). Indeed, interspecific interactions may be more costly at lower latitudes where, for example, organisms invest more energy or resources in combating parasitism (Møller 1998). Moreover, differences in range boundaries at the high- and low-latitude portions of species ranges are consistent with the assumption of greater interspecific effects at low latitudes and greater abiotic controls at high latitudes (Kaufman 1998). That is, range boundaries in extratropical areas were more linear and adherent to latitudinal parallels compared with range boundaries in more equatorial areas. Importantly, none of these mechanisms alone can generate the latitudinal gradient of richness. Each requires an underlying pattern in diversity or the factors that effect it before becoming operational.

The population theme requires a latitudinal pattern in demographic characteristics (e.g., individuals within populations or population dynamics) that must be produced by some other factor, such as species packing. Empirical support for the appropriate latitudinal gradients in population characteristics is not pervasive. For example, monogenean and digenean parasites of marine fishes did not have smaller population size nor were their niches narrower in the tropics (Rohde 1978a).

The evolutionary rate theme has been invoked to produce latitudinal gradients of richness (Rosenzweig 1975). For example, high speciation rates have been linked to the great richness of the lowland wet tropics (Brown 1988). Other mechanisms (such as the larger area, increased productivity, and greater environmental predictability) have been invoked as causes for these purported high speciation rates and low extinction rates in the tropics (Rosenzweig 1975). From a methodological

perspective, the accurate measurement of rates is a challenge in the evaluation of these hypotheses (Brown 1988).

We consider six hypotheses for further elaboration. These have the most support and potential, are least easy to refute based on current information, or are general and synthetic. We do not elaborate further on recently advanced hypotheses (Table 1) that have not been evaluated in the literature.

Geographic Area Hypothesis

Although this mechanism was originated by Terborgh (1973), it has been most developed and amplified as a hypothesis by Rosenzweig (1995). The primary tenet is that the tropics support more species than other regions because they comprise more area. A secondary tenet is that elevated productivity in equatorial regions along with enhanced zonal bleeding in the tropics interact with areal effects to produce a gradient of increasing richness with decreasing latitude. Although considerable controversy surrounds the hypothesis (Rohde 1997, 1998; Rosenzweig & Sandlin 1997), it does not question if areal mechanisms increase richness; rather, it focuses on the degree to which area is the dominant factor effecting the latitudinal gradient (Willig 2001).

Two aspects of the earth's geometry predispose area to increase from polar to tropical areas. First, the earth is essentially a sphere, and the circumference of latitudinal parallels is greatest at the equator and becomes progressively smaller toward the poles. Consequently, the area of a latitudinal band of fixed width is greatest at 0° and least at the poles. Second, the distribution of Tropical, Temperate, and Polar Zones is symmetrical around the equator. More specifically, northern and southern Polar Zones are disjunct, separated by the intervening temperate and tropical areas. Similarly, northern and southern Temperate Zones are disjunct, separated by intervening tropical areas. In contrast, northern and southern Tropical Zones are adjacent, straddling the equator to form a contiguous tropics. If the earth's landmasses or bodies of water were randomly distributed across the globe then the area of available land or water would gradually increase from polar to tropical regions. Thus, diminished area and increased isolation of extratropical areas initiates a concomitant gradient of species richness.

More pervasive than the latitudinal gradient is the observation that species richness increases with area. As the area of a region increases, so too does the number of habitats, biomes, or biogeographic provinces within it. Similarly, as the area of a region increases, so too does the area of its constituent habitats, biomes, or provinces. Larger areas support more individuals and populations of a species, and reduce the likelihood of extinction. Larger areas have a higher likelihood of containing geographic barriers to gene flow, which would enhance speciation rates. Larger areas will have more diverse habitats facilitating the development of specialization, adaptation, and speciation. On average then, a larger area potentially will support more richness at a variety of scales (i.e., alpha, beta, and gamma diversity) and will certainly enjoy higher overall species richness.

Evidence regarding this hypothesis is inconclusive. Rosenzweig (1995) and Rosenzweig & Sandlin (1997) provided evidence in support of the hypothesis. Regardless of latitude, larger biotic provinces contain more taxa (species, genera, and families) than do their smaller counterparts. Moreover, species richnesses from the same biome but different continents or provinces vary as a function of their latitudinal extents. Ruggiero (1999) also provided support for the hypothesis in a comprehensive statistical analysis of mammalian gradients in South America in which she controlled for the presence of tropical species in extratropical biomes. In contrast, Rohde (1997, 1998) does not consider area to drive the latitudinal gradient. For example, smaller tropical areas of Eurasia contain far more species of freshwater fishes than do larger temperate regions. In addition, the expansive deep-sea biome with essentially constant temperature supports only a fraction of the species that occur in its much smaller tropical counterpart. In North America, the greatest continental width occurs at relatively high latitudes, and latitude and area are correlated positively, whereas in South America the greatest continental width occurs at equatorial regions, and latitude and area are correlated negatively. Nonetheless, for mammals in North America and in South America, area had little unique explanatory power as compared with latitude, and the latitudinal gradient of richness was significant and steep for each continent, even when the effects of area were removed in analyses of covariance (Kaufman & Willig 1998).

Productivity Hypothesis

The idea that energy limits richness dates back at least as far as Hutchinson (1959). Pianka (1966) wrote that "greater production results in greater richness, everything else being equal." Wright (1983) advanced the species-energy hypothesis as a more general extension of the species-area theory of MacArthur & Wilson (1963, 1967). The productivity hypothesis posits that the annual input of solar radiation determines energy availability, productivity, and biomass, and is tightly related to latitude in an inverse manner (Robinson 1966). Measures of productivity, such as actual evapotranspiration (AET), generally are correlated to species richness, but not in all organisms and generally not as highly as is potential evapotranspiration (PET). For example, in North America, neither bird nor mammal richness exhibited high correlations with AET (Currie 1991). For other organisms, such as North American trees and amphibians, the correlation between AET and species richness is quite high (Currie 1991).

Although a positive relationship between productivity and richness seems likely, at least for an appreciable portion of the gradient, the productivity hypothesis has not been accepted generally as an important cause of geographic patterns of species richness (Brown & Gibson 1983). Currie (1991) identified a critical shortcoming of the productivity hypothesis. It fails to elucidate a mechanism as to how or why species richness would increase to a maximum set by energy availability, as opposed to population densities simply increasing in magnitude. Although highly productive environments can exhibit great richness, they also may exhibit low

richness in some situations (MacArthur 1972). Indeed, little generality about the form of the relationship between species richness and productivity (i.e., positive linear, negative linear, modal) exists (Mittelbach et al. 2001, Waide et al. 1999) other than the view that it is scale dependent (Gross et al. 2000, Pastor et al. 1996, Scheiner et al. 2000, Scheiner & Jones 2002). Thus, productivity alone cannot explain latitudinal gradients of richness.

Ambient Energy Hypothesis

This hypothesis considers the input of solar energy to create a physical environment that affects organisms through their physiological responses to temperature. Ambient energy essentially serves as an umbrella hypothesis under which other explanations, such as climatic stability, environmental stability, environmental predictability, seasonality, and harshness, are subsumed. This hypothesis is based on the concept that environments at high latitudes have mean conditions farther from organismal optima (e.g., their thermal neutral zones) than do their low-latitude counterparts. In addition, high-latitude environments are thought to be more variable and seasonal than are those at low latitudes. Based on temperature records from climatological stations throughout the New World, high latitudes evinced lower mean temperature, colder winter extremes, higher annual variability, and shorter growing season as compared with lower latitudes (Kaufman 1998). This is equivalent to the idea that higher latitudes are harsher for organisms than are lower latitudes. Species-poor habitats often have physiologically harsh and unpredictable environmental conditions that require special and costly adaptations (Brown 1988). Rohde (1992) considered the harshness hypothesis to be circular. Nonetheless, physiological characteristics can be used to assess favorableness instead of simply reasoning that low latitudes are favorable because there are many tropical species and high latitudes harsh because there are few polar species. For example, it is more physiologically costly to live at high latitudes than low latitudes because the ambient temperature in polar regions is outside the thermal neutral zone of many organisms for a majority of the year.

Several measures of ambient energy are highly correlated to species richness. For example, sunshine and temperature were the primary underlying factors affecting butterfly richness in Great Britain, as a consequence of basking and physiological requirements (Turner et al. 1987). Moreover, PET, a measure of ambient energy, was generally correlated with species richness of trees, amphibians, reptiles, birds, and mammals in North America (Currie 1991, Currie & Paquin 1987).

Rapoport-Rescue Hypothesis

Rapoport's rule is a pattern in which the size of the distributional ranges of species is related inversely to latitude (Rapoport 1975, Stevens 1989). A diversity of taxa that inhabit aquatic and terrestrial environments exhibited the pattern (e.g., mammals, reptiles, amphibians, fish, crayfish, amphipods, mollusks, and trees). When proposed, Rapoport's rule was designed as a mechanism to underlie the

latitudinal gradient of richness. Because seasonal variation at high latitudes is great, organisms with broad climatic tolerances will be favored by natural selection in these areas. Broad tolerance not only allows organisms to persist through time in a particular locale, but also results in the possession of large ranges. In contrast, organisms from more tropical latitudes generally have narrower climatic tolerances and more restricted ranges. Furthermore, the narrower tolerances of tropical organisms cause the environment to be more heterogeneous from their perspective, and they are more likely to disperse or spillover into unfavorable areas. Overall species richness is augmented by the addition of "accidentals," species that normally would not persist but are "rescued" by continual dispersal from nearby favorable areas. That many taxa exhibited both the latitudinal gradient of richness and Rapoport's rule suggested a link between them; furthermore, taxa that did not exhibit a latitudinal gradient were generally exceptions to Rapoport's rule.

Rapoport's rule is more uniformly exhibited by taxa in the Northern Hemisphere than in the Southern Hemisphere. Moreover, the rule is less substantiated in the tropics compared with the Temperate Zone (Gaston et al. 1998). Indeed, empirical evidence and quantitative modeling (Colwell & Hurtt 1994, Lyons & Willig 1997, Taylor & Gaines 1999, Willig & Lyons 1998) together suggest that the logic underlying the Rapoport-rescue hypothesis is flawed or only applicable under restrictive circumstances (Rohde 1996). Moreover, some taxa that exhibit a marked latitudinal gradient of richness do not exhibit Rapoport's rule (e.g., New World bats and marsupials—Lyons & Willig 1997, Willig & Gannon 1997, Willig & Selcer 1989), diminishing the likelihood that the Rapoport-rescue hypothesis represents a general mechanism producing latitudinal gradients of richness.

Evolutionary Speed Hypothesis

Rohde (1992) proposed the evolutionary speed hypothesis, which holds that species richness increases toward the tropics because of temperature-induced increases in rates of speciation. That is, high temperature enhances evolutionary speed. Latitudinal patterns of temperature result in shorter generation times, higher mutation rates, and accelerated selection pressure in the tropics, which combine to enhance rates of speciation, and as a consequence, species richness (Rohde 1992). His view diverged from those who support the ambient energy hypothesis because only under equilibrial conditions and community saturation would available energy be able to effect a latitudinal gradient. Such conditions have not been shown and would be challenging to document (Rohde 1992).

The number of generations per year is related negatively to latitude in some taxa; however, short generation times do not always lead to faster evolutionary rates (Rohde 1992). Although little actual evidence supports or refutes the mechanistic underpinnings of this explanation, Jablonski (1993) suggested that the tropics have been a source of evolutionary novelty throughout geologic time as evidenced by the higher origination rates of post-Paleozoic marine orders in equatorial areas compared with temperate areas. However, a recent quantitative analysis based on

phylogenetically independent contrasts of rates of evolution in latitudinally separated pairs of bird species provided no support for the contention that rates of molecular evolution increase toward the tropics (Bromham & Cardillo 2003). If similar research and data for other taxa fail to support the negative association between evolutionary rates and latitude, the evolutionary speed hypothesis can be removed as a plausible mechanism that effects the latitudinal gradient in species richness.

Geometric Constraints Hypothesis

The geometric constraints hypothesis originated as a consequence of a radically different approach for understanding the latitudinal gradient—one that does not require environmental gradients to be associated with changes in latitude and one that does not require the biota to respond to environmental gradients if they do exist. Colwell & Hurtt (1994) suggested that "nonbiological" latitudinal gradients of species richness could be produced as a consequence of the random placement of species ranges within a bounded domain. A bounded domain is an area circumscribed by a physical (e.g., continental coastlines for terrestrial species) or a physiological barrier (e.g., salinity levels for freshwater fish) that restricts the distribution of species within a taxon to a subset of the earth's surface. If the world is effectively unbounded, the random placement of species ranges fails to produce a gradient (i.e., produces a line with zero slope for the relationship between species richness and latitude). This condition is the equivalent of the null hypothesis, a statement that is inherent to all statistical assessments of latitudinal gradients. If the world is characterized by boundaries, gradients in richness of various types are produced, depending on a number of constraints.

Indeed, the sizes of species ranges as well as their central locations are the proximate determinants of any latitudinal gradient. Consequently, a full spectrum of simulation models has been developed that reflects various constraints on the placement of species ranges within a bounded domain (Colwell & Hurtt 1994, Colwell & Lees 2000). The three general categories of such null models include those that are (*a*) unconstrained, (*b*) constrained by the location of range midpoints, and (*c*) constrained by the distribution of range sizes. In general, all of these models produce latitudinal gradients with peaks in richness at mid-domains. The models differ with respect to predictions concerning the rate of increase in richness toward the mid-domain, the magnitude of maximum richness, and the kurtosis of the latitudinal gradient of richness. In addition to simulation approaches, analytical models also suggest a latitudinal gradient with mid-domain peaks in species richness (e.g., Lees et al. 1999, Willig & Lyons 1998).

Unlike all the other hypotheses concerning the latitudinal gradient in species richness, geometric constraint models make quantitative predictions in terms of the latitudinal location of the richness peak, the form of the latitude-richness relationship, and in the richness of species at any particular latitude. Empirical support for the geometric constraints model is increasing (see Hawkins & Diniz-Filho 2002 for an alternate view). For example, Willig & Lyons (1998) applied a binomial model to the New World and found that it produced a tropical peak in species

richness. Moreover, they compared their predictions to empirical data for bats and marsupials and found that much of the latitudinal variation in species richness was related to the random placement of species ranges, depending on the location of hard boundaries. For bats, between 67% and 77% of the variation in richness was accounted for by the model. Similarly for marsupials, between 35% and 94% of the variation in richness was accounted for by the model. Importantly, empirical patterns deviated from predictions for each biota in a different way, providing additional insights not possible with other models. In particular, marsupials deviated from model predictions by being less rich at all latitudes than predicted by the model, whereas bats deviated from model predictions by being richer in the tropics and more depauperate in temperate regions. Other biotas exhibited latitudinal gradients that conform to the predictions of various geometric constraint models, including rodents in the deserts of the American Southwest (McCain 2003) and endemic rainforest butterflies, frogs, rodents, tenrecs, chameleons, and birds in Madagascar (Lees et al. 1999).

Finally, geometric constraint models make a unique prediction about the latitudinal gradient that is not shared by any of the other hypotheses and often is in opposition to them (Willig & Lyons 1998). That is, species whose distributions are wholly contained within any geographic domain—even randomly determined hard boundaries—should exhibit a mid-domain peak in richness. Bats and marsupials in the New World conformed to these predictions for 100% and 95% of 20 random locations that extended at least 20° of latitude and contained at least 20 species in the biota of interest. The application of two-dimensional geometric constraint models has successfully accounted for a significant amount of the variation in bird species richness in southern Africa (Jetz & Rahbek 2001, 2002). It has been less successful for South American raptors (Diniz-Filho et al. 2002b), Nearctic birds (Hawkins & Diniz-Filho 2002), and New World mammals (Bokma et al. 2001).

Predictions from geometric constraint approaches may act as a null model against which empirical data are evaluated regarding the latitudinal gradient. Nonetheless, Hawkins & Diniz-Filho (2002) considered the hypothesis to be flawed because the assumption that ranges exist independently of the environment or that ranges are randomly placed has no theoretical justification. Of course, such assumptions of neutrality are inherent to geometric constraint models and null models in general. Moreover, neutral mechanisms as well as deterministic mechanisms can operate simultaneously to produce patterns, and need not be constrained to represent mutually exclusive phenomena (Hubbell 2001), a view that is gaining appreciation in ecology and biogeography. An alternative view is that each species in a biota is unique by its very nature. It responds to the multivariate environmental template in different ways throughout its distribution and in a manner unlike any other species. Numerous examples concerning the diversity of factors affecting species distribution are the fodder for textbooks in ecology and biogeography (e.g., Krebs 1994). Moreover, studies of the response of species to the last glaciation cycle support this view in that taxa shift their ranges in species-specific and unpredictable manners given present knowledge of their niche dimensions (e.g., Holman 1995 for North American herpetofauna; Valentine & Jablonski 1993 for

marine mollusks; Davis & Shaw 2001 for North American trees; Lyons 2003 for North American mammals). Correspondence between empirical gradients and geometric constraint models may not reflect the role of chance in determining the distribution of species per se. Rather, it may reflect the many and unpredictable ways in which evolutionary processes have molded the adaptations of species so that they respond to the environment in a multitude of ways (Lyons & Willig 1997).

Distinguishing Among the Hypotheses

The problem of distinguishing among hypotheses concerning the latitudinal gradient of richness is that most represent conceptual models rather than quantitative models and only make the qualitative prediction that species richness should increase with decreasing latitude. Moreover, many of the mechanistic factors associated with different hypotheses are shared or correlated; consequently, indirect tests are problematic and controvertible. However, progress has occurred in reducing the number of likely causative mechanisms (e.g., Willig 2001; D.M. Kaufman & J.H. Brown, in review). By capturing the fundamental nature of over 30 hypotheses, and categorizing them into themes, we provide a reasonable springboard from which to launch future investigations of the mechanistic bases of the gradient. The detailed review of a number of popular, controversial, or promising hypotheses will hopefully direct future research in ways that will challenge contemporary perspectives or corroborate mechanistic explanations of nature's longest recognized and most pervasive pattern. Nonetheless, advancing ecological and evolutionary understanding of the bases of the latitudinal gradient requires adoption of new or additional conceptual, empirical, and analytical approaches.

CONCLUSIONS

The wide variety of data that have been collected across taxa, space, time, and scale has allowed ecologists to assemble considerable evidence in support of the current paradigm (Figure 1). Scale effects generally are of two types. Those related to extent can result in considerable variation in the form and parameterization of the latitudinal gradient. In contrast, those associated with focus usually result only in variation in the parameterization of the classical pattern of richness increasing toward the equator. Further collection of data will increase the likelihood that we truly understand the extent to which the pattern is universal and the contexts in which exceptions occur. Similarly, expanded focus on causes of elevational or bathymetric gradients, known to be affected by similar environmental parameters as those likely affecting the latitudinal gradient, will lead to a more mature body of theory regarding diversity in general, and the latitudinal gradient in particular.

Although additional pattern analysis will enrich our characterization and knowledge of the latitudinal gradient of diversity, the current challenge is to elucidate a convincing, mechanistically based theory to explain the generation and maintenance of the gradient, including the conditions that account for the current

exceptions (e.g., Willig 2001, Whittaker et al. 2001). Clearly, no single mechanism appears adequate to account for the taxonomic, geographic, and temporal ubiquity of the latitudinal gradient. Pianka (1966) believed that combining of hypotheses should be avoided because it would be "less testable and useful." However, if multiple factors vary in concert with latitude and interact to cause the latitudinal gradient of richness, it is doubtful that the evaluation of these factors in isolation will bring about meaningful progress (Rosenzweig 1975; Willig 2001; D.M. Kaufman & J.H. Brown, in review).

Because beta diversity connects levels of richness at local and regional levels, it is a key to understanding scale dependence. Consequently, renewed efforts to understand how the environment molds beta diversity will contribute significantly to advancing a number of subdisciplines in macroecology, especially those dealing with gradients such as latitude, elevation, depth, or productivity. At the same time, a careful consideration of the consequences of stochastic processes operating in a bounded world must be incorporated into hypothesis testing and the construction of predictive models, even those with strong mechanistic underpinning. Indeed, only a few hypotheses have made explicit predictions, about the qualitative or quantitative nature of the richness gradient or about other macroecological characteristics, such as range size distribution, abundance, and diversity.

Recently amplified hypotheses are more synthetic in nature (e.g., Whittaker et al. 2001). Indeed, synthetic hypotheses should employ multiple mechanistic features, such as the incorporation of ambient energy, productivity, and interspecific interactions, and should make explicit predictions, an approach advanced by Kaufman (1995, 1998). As Gaston (2000) stressed, a "predictive theory of species richness" is still distant, but work over the past decade characteristically exhibits a much greater emphasis on predictiveness. Furthermore, research that contributes to an understanding of the latitudinal gradient is departing from a narrow focus on latitude, per se. Two schools of thought are emerging. One continues to examine factors in an explicitly latitudinal framework (e.g., Koleff & Gaston 2001). The other examines richness and causative mechanisms across spatial dimensions without including latitude as a particular factor in the framework (e.g., Allen et al. 2002, Hawkins et al. 2003, Hurlbert & Haskell 2003). As with any complex system (Rosenzweig 1975), it is unlikely that any one variable will entirely account for latitudinal gradients of richness. Instead, several factors will inform a comprehensive mechanism that applies to most biotas in most places during much of evolutionary time (Gaston 2000). As such, we provide a simple conceptual model (Figure 5) that links mechanisms from a variety of hypotheses, and suggest how each would affect alpha, beta, and gamma diversity. We end with a litany of recommendations for future research in terms of empirical, statistical, and conceptual approaches.

Recommendations for Conceptual Approaches

■ To guide future research, an overarching model with hierarchical representation of particular mechanisms (e.g., Figure 5) should comprehensively reflect

the primary and secondary gradients that cause or modify spatial patterns of diversity.

- Models should be developed that make explicit predictions about how various metrics of diversity (e.g., richness, evenness, dominance, turnover) at multiple spatial or ecological scales (e.g., alpha, beta, or gamma diversity) are associated with mechanistic processes.

- Synthetic linkages are needed between models associated with gradients of richness and models associated with other macroecological characteristics (e.g., body size, range size, niche dimensions).

- The ramifications of particular hypotheses should be explored to identify unique quantitative or qualitative predictions that differ from those associated with competing hypotheses.

- Advocates of particular hypotheses should postulate critical tests that can be addressed by empirical evidence (hypotheses that cannot be wounded fatally are not vital or useful).

- The assumption that increased energy leads to elevated species richness rather than simply more individuals needs to be validated from first principles.

Recommendations for Empirical Approaches

- The spatial focus of analyses (e.g., point diversity versus alpha diversity versus gamma diversity) needs to be explicit and clearly linked to mechanisms at relevant spatial scales.

- Empirical evidence for gradients in turnover at a variety of ecological scales (i.e., local beta diversity, beta diversity, and delta diversity) are needed to understand the spatial dynamics of diversity, and how heterogeneity affects broad scale patterns.

- Additional empirical research on latitudinal gradients in alpha diversity are needed to guide investigation of how variation in local conditions affects the richness of communities.

- Research should be amplified to include latitudinal gradients in weighted measures of diversity (e.g., species diversity, evenness, and dominance) and to contrast these to patterns in species richness.

Recommendations for Analytical Approaches

- Analytical methods that minimize the effects of spatial autocorrelation on analyses of latitudinal gradients need to be developed and deployed.

- Broader use of simulation approaches and dynamic modeling is needed to decouple the effects of confounding variables in assessments of causative mechanisms.

■ Statistical testing of the mechanistic basis of the latitudinal gradient should be undertaken in the context of geometric constraint models in two dimensions, including more comprehensive analyses of residuals.

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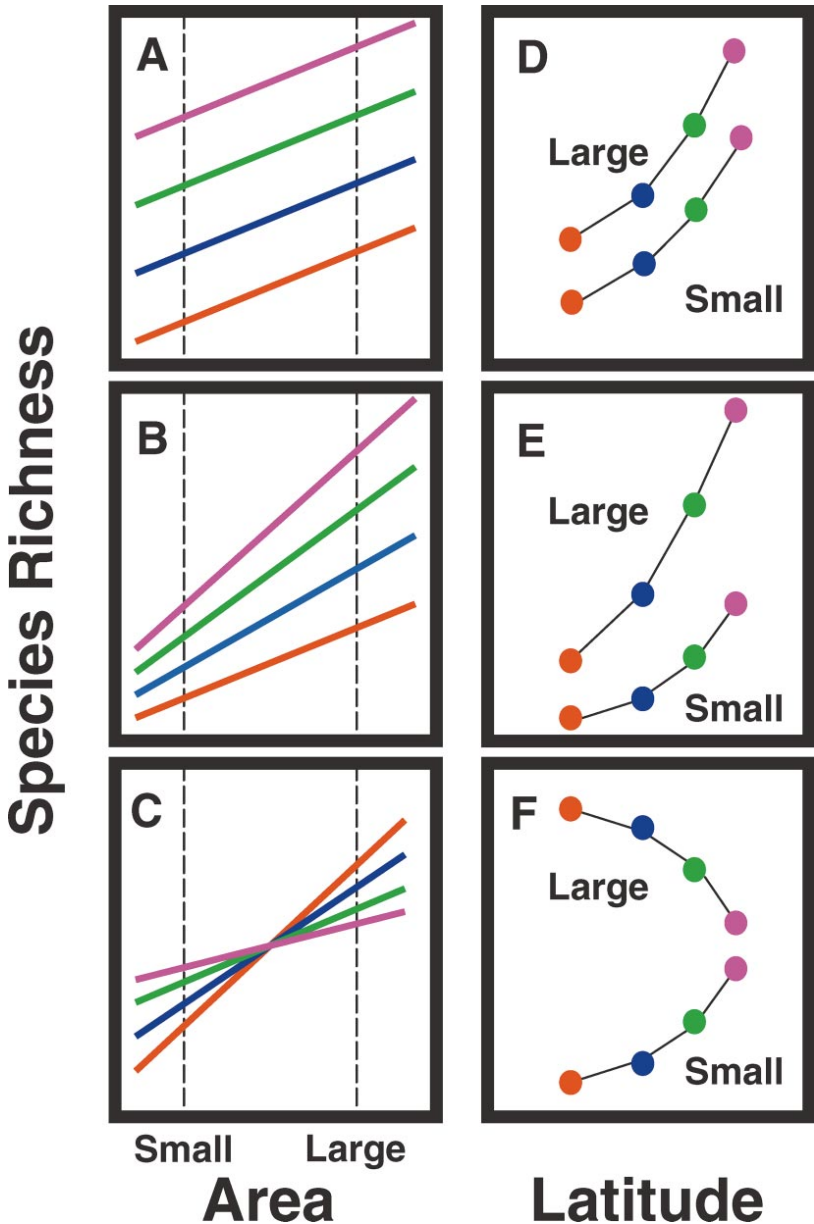Wright DH. 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41:496–506

Figure 1 The latitudinal gradient in richness is scale independent when the species-area relationship is parallel at all latitudes (*A* and *D*). The latitudinal gradient is rank-invariant when the species area relationships do not intersect within 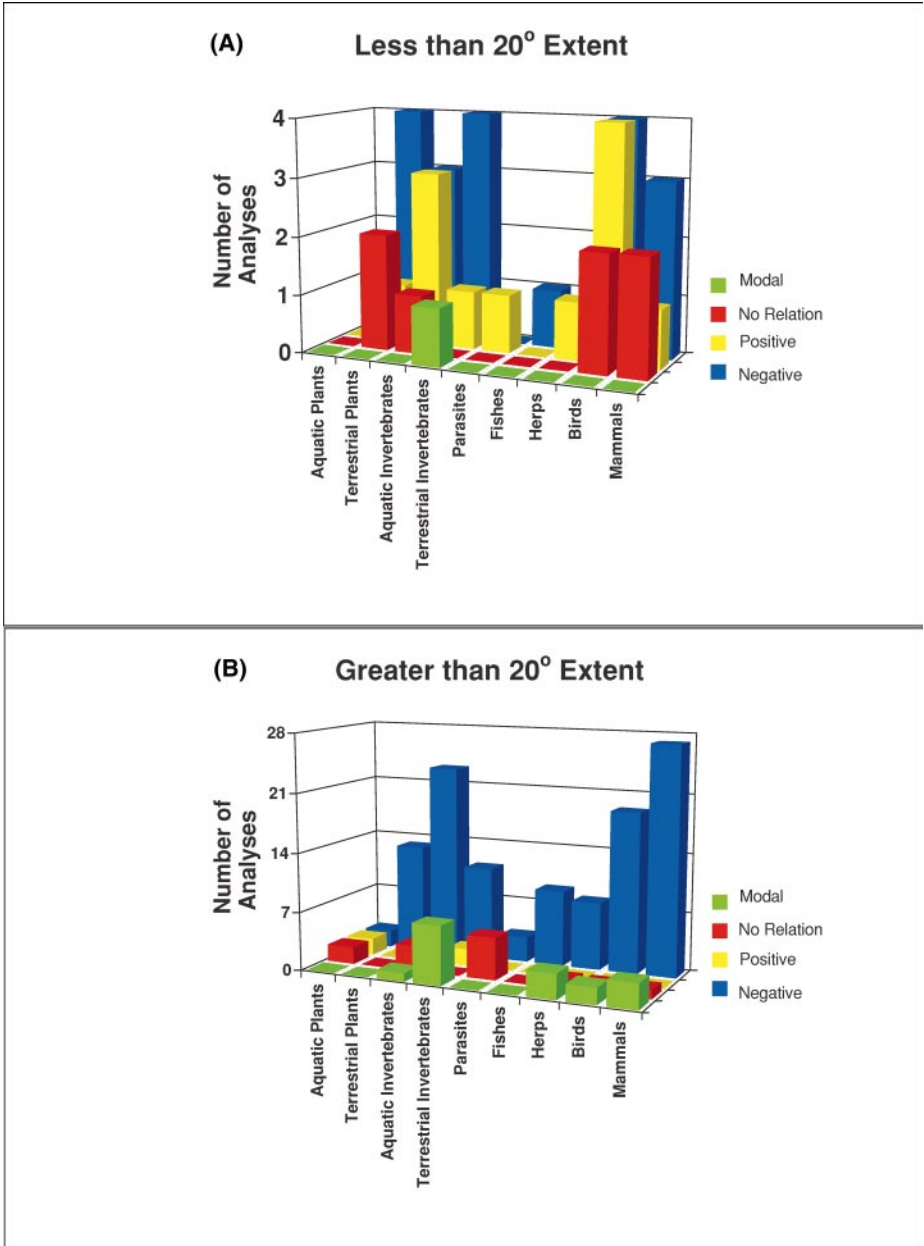the domain of areas considered in an analysis (*B* and *E*). The latitudinal gradient is neither scale- nor rank-invariant when the species area relationships intersect within the domain of areas considered in an analysis (*C* and *F*).

Figure 3 A cross-classification of analyses (see electronic appendix for details) of the latitudinal gradient of richness by latitudinal extent (*A*, narrow [<20°]; *B*, broad [≥20°]) and pattern (increasing toward the tropics [positive], decreasing toward the tropics [negative], modal, and nonsignificant).
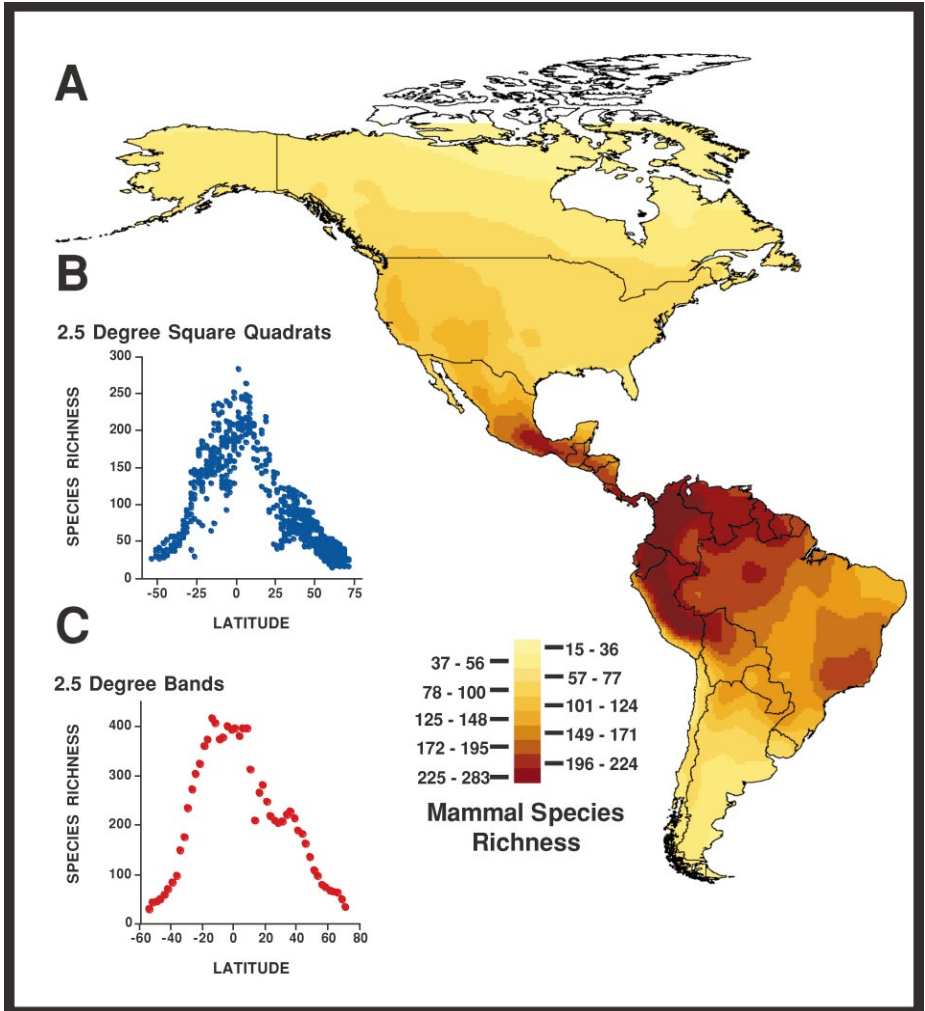
Figure 4 Spatial gradient of mammalian species richness in the continental New World for cells defined by 2.5° parallels and meridians. (*A*). Interpolated richness values in the map were created using the tension spline function in the Spatial Analyst extension to ArcGIS 8.2. Graphic representation of the latitudinal gradient in species richness for those same data (negative values for latitude indicate southern parallels), based on 2.5° cells (*B*) and 2.5° latitudinal bands (*C*). Data from Kaufman & Willig (1998).
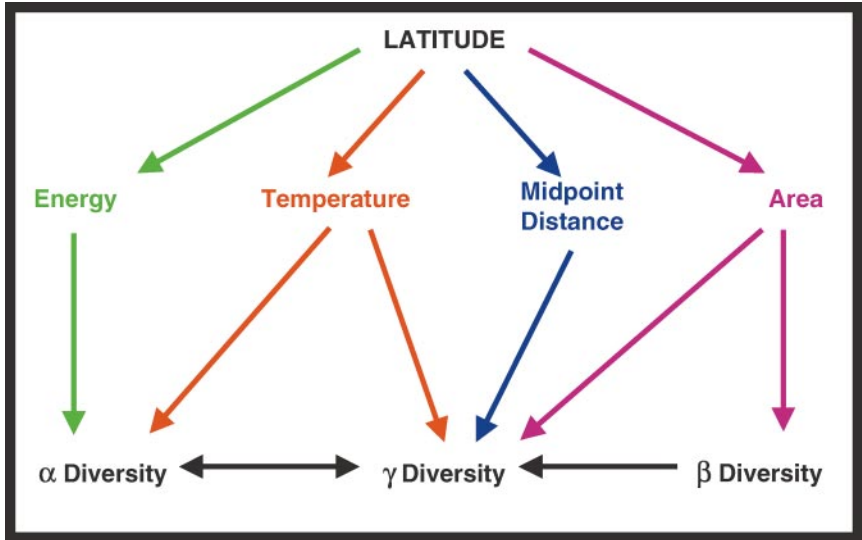
Figure 5   Conceptual model indicating the avenues by which mechanistic factors affect alpha, beta, or gamma diversity in the context of broad latitudinal gradients. Measures of alpha diversity are assumed to be based on areas of equal size or to be determined by asymptotic estimators.