

Beyond Species Richness: Biogeographic Patterns and Biodiversity Dynamics Using Other Metrics of Diversity

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Introduction

Biological diversity is difficult or perhaps impossible to measure using a single metric. To most people the term “diversity” is synonymous with “variety,” and formal definitions of the term biological diversity try to capture this “variety of life” by including everything from genetic to ecological diversity (Gaston 1996). Yet at present our knowledge of spatial and temporal patterns of biodiversity is based almost entirely on one metric: taxonomic richness. From biogeographic patterns to extinction intensities, all are quantified primarily by using numbers of species or higher taxa. Other measures of biological diversity do tend to correlate with species richness, so that an area with a large number of species is also likely to have, say, higher genetic, morphological, and ecological diversity than an area with few species. However, we also know that the relationship between taxonomic richness and other diversity metrics is often complex and non-linear, and one may not be a good predictor of the other (Foote 1997; Roy and Foote 1997; Wills 2001; but see Williams and Humphries 1996).

In the absence of actual measures of these other facets of diversity such as morphologic, functional, phylogenetic, and ecological relationships, we know little about the spatial and temporal distributions of the “variety of life.” More importantly, replacing simple taxon numbers with metrics that attempt to incorporate some measure of differences among species may reveal spatial and temporal trends not evident from taxon counts, and provide richer insights into the dynam-

ics underlying biogeographic and macroecological patterns. In this chapter we use a number of case studies to show how incorporating morphological and functional information (1) changes how we view biogeographic patterns, and (2) helps us better test hypotheses about the processes underlying many types of diversity patterns. We use the morphological and functional examples simply because we are familiar with those metrics, not because we think they are more important than other measures such as genetic or phylogenetic diversity. In our view, the major challenge facing biogeographers is to replace spatial models that primarily incorporate taxon counts with ones that will more fully capture the true and manifold varieties of life.

Quantifying Patterns

Spatial Patterns of Morphological Diversity

Morphological diversity is commonly defined as some quantitative estimate of the empirical distribution of taxa in a multivariate space (morphospace) where individual axes represent measures of morphology (Foote 1997; Roy and Foote 1997; Eble 1998; McGhee 1999; Ciampaglio et al. 2001; Wills 2001; MacLeod 2002). Since most organisms have an indefinite number of potentially quantifiable morphological traits, analyses generally focus on quantifying specific aspects of morphology rather than tackling the impossible task of measuring total morphological diversity (Roy and Foote 1997).

Most species are differentiated on the basis of morphology, and a simple relationship between taxonomic richness and morphological diversity might be expected. Empirical studies of this question are scarce but analyses for birds, bats, lizards, and fishes suggest a general tendency for morphospace volume to increase with taxonomic richness, while nearest-neighbor distances within these morphospaces tend not to vary with richness (Ricklefs and Miles 1994). This pattern holds even for tropical-temperate comparisons. For example, overall morphological diversity of North American mammals, based on skull, dentary, and long-bone traits was higher in tropical assemblages compared to temperate ones, but nearest-neighbor distances showed no significant relationship with species richness (Shepherd 1998); comparable results were obtained by Ricklefs and O'Rourke (1974) in a pioneering study of tropical and temperate assemblages of night-flying moths. Similarly, many of the novel morphologies characterizing tropical taxa of marine molluscs are absent from extratropical areas, and these differences, which correlate roughly to latitudinal differences in richness, have been attributed to differences in predation pressure along latitude, or changes in the physical environment (Vermeij 1978, 1987a; Vermeij and Signor 1992). The tendency for tropical genera of marine molluscs to be species-poor relative to high-latitude genera (Roy et al. 1996) also suggests that tropical species are generally more dispersed in morphospace, but exceptions are known and this is yet to be tested directly.

Despite these rough correlations, morphologic and taxonomic diversity are not so tightly correlated that one can reliably serve as a proxy for the other, and discordances between morphological and taxonomic diversity can raise interesting new questions. For example, a comparison of longitudinal trends of species richness and morphological diversity of Indo-Pacific gastropods of the family Strombidae shows that morphological diversity in the most species-rich regions is no higher than that in regions with half the number of species. In other words, volume of morphospace occupation, as defined by shell shapes, initially increases rapidly with species richness but the rate of increase slows down as more species accumulate (Figure 8.1; Roy et al. 2001; Neige 2003). For the same data, variance in morphospace—a measure of morphological disparity between species—was again not predictable from species richness alone; some areas with relatively few species exhibit disparity values comparable to those with highest species richness (see Figure 8.1). Strombid gastropods are commonly cited as a classic example of the Indo-Pacific species richness gradient, with the Indo-Malayan region having the highest species richness (Briggs 1974 and this volume; Vermeij 1987a and this volume). But when morphology is used as the diversity metric, the longitudinal gradient looks very different from the traditional view (Figure 8.2).

The discordance between taxonomic and morphological diversity is also apparent over evolutionary timescales and is most striking during episodes of intense diversification such as the Cambrian explosion of marine metazoans, when a broad range of morphological variety is established well in advance of peak taxonomic diversity (reviewed in Foote 1997, Valentine et al. 1999, and Wills 2001). These findings suggest that, when analyzed on global scales over millions of years, clades can reach longstanding limits to their morphological diversity—which need not be permanent or absolute—while continuing to accumulate taxonomic richness through time, presumably by increasing the density of morphospace occupation over time. These limits have been attributed to intrinsic factors related to development and to extrinsic factors relating to ecological limitation (e.g., Valentine 1995; Eble 1998; Valentine et al. 1999; Jablonski 2000), but definitive tests of these alternatives remain elusive.

Body size is another aspect of morphology that is of interest from a biogeographic perspective. The expected relationship between species richness and body size has been much debated. For example, some argue that the positive scaling of energy requirements of species with body size should produce an inverse relationship between species richness and body size (Cousins 1989; Blackburn and Gaston 1996). This suggests that average size should increase with latitude for groups that show a strong latitudinal gradient in species richness. On the other hand, the species-energy hypothesis suggests that high-latitude assemblages should have low species richness and smaller body sizes due to the reduced energy availability relative to equatorial regions (Turner and Lennon 1989; Cushman et al. 1993). Empirical analyses have yielded mixed results. Among ectotherms, some groups show

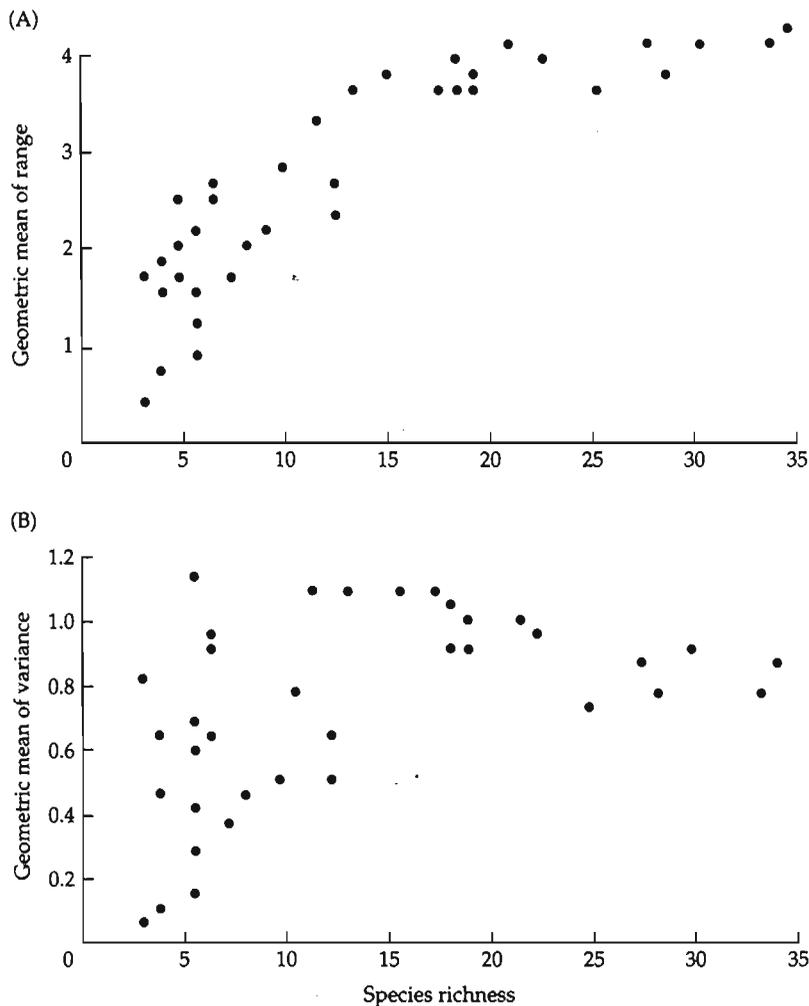


FIGURE 8.1 Relationship between species richness and morphological diversity in strombid gastropods (Family Strombidae). Morphological diversity was quantified using elliptical Fourier analyses of shell shapes. (A) Morphological diversity is defined as the geometric mean of the range of scores on the first six axes of a principal component analysis. This measure correlates with the volume of morphospace occupation. (B) Morphological diversity as the geometric mean of the variance of scores on the same six PCA axes, illustrating the dispersion of species in morphospace. (From Roy, Balch, and Hellberg 2001.)

a positive relationship between size and latitude, while other groups show a negative relationship or none at all (Schoener and Janzen 1968; Cushman et al. 1993; Barlow 1994; Hawkins 1995; Hawkins and Lawton 1995; Kaspari and Vargo 1995; Roy, Jablonski, and Martien 2000; Roy and Martien 2001). A similar situation also holds true for endotherms (McNab 1971). This lack of a consistent relationship between body size and latitude (and, indirectly,

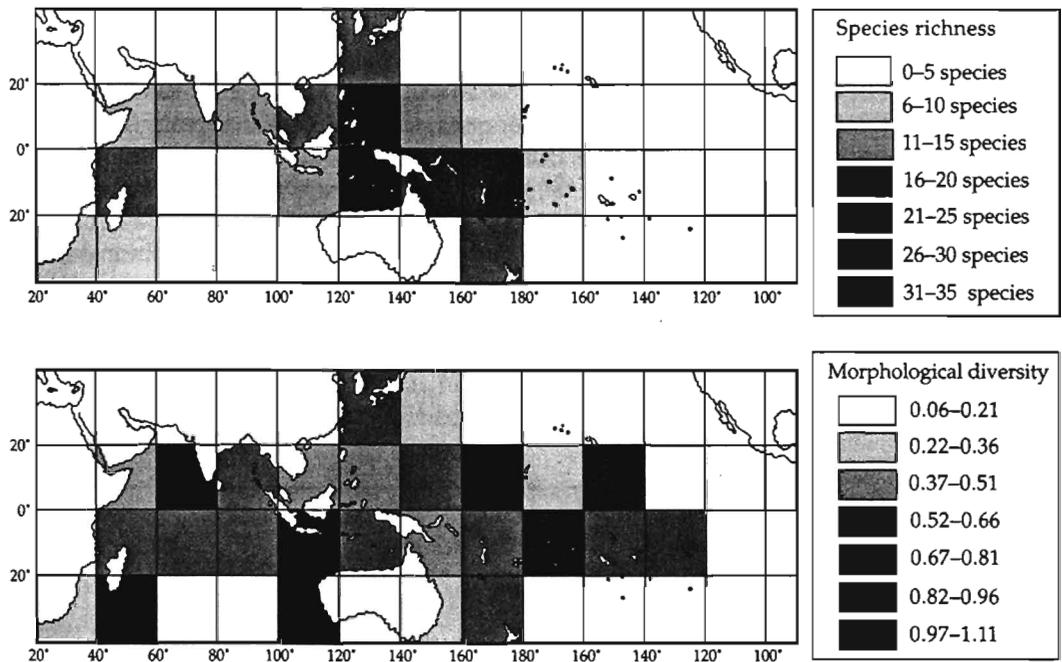


FIGURE 8.2 Spatial patterns of taxonomic and morphological diversity of strombid gastropods across the Indo-Pacific. Morphological diversity represented by geometric mean of the variance of scores on the first six PCA axes as in Figure 8.1B. Note the poor correlation between spatial patterns revealed by the two diversity metrics. (From Roy, Balch, and Hellberg 2001.)

species richness) indicates that biogeographic patterns based on species richness are poor proxies for the biogeography of body size, one of the most important and interesting organismic traits.

Functional Groups and the Latitudinal Diversity Gradient

The latitudinal diversity gradient, with species-rich tropics and depauperate high latitude regions, is perhaps the most striking large-scale biogeographic pattern of all. This pattern is common on land and in the oceans and across many taxonomic groups, but despite a multitude of proposed hypotheses, the processes underlying this gradient remain largely unknown (Rohde 1992; Gaston 2000; Turner and Hawkins, this volume). Part of the problem may be that, despite the progress noted above, we do not know whether high species richness in the tropics necessarily translates into proportionately high morphological, functional, genetic, or phylogenetic diversity. Even clades that show very similar latitudinal trends in species richness may differ strongly in their patterns of functional or morphological diversity along the same gradient. These differences are important since they not only provide a macroeco-

logical framework for understanding the dynamics underlying the latitudinal diversity gradient but also, as shown below, can reveal differential responses among functional groups to the same environmental variable. Testing hypotheses about the processes driving latitudinal patterns of diversity using only total species richness of a group obscures these differences.

Marine molluscs, one of the most diverse groups of animals living on the continental shelves of the world's oceans (<200 m depth), show a strong latitudinal diversity gradient in the Northern Hemisphere (Roy, Jablonski, and Valentine 1994, 1998, 2001).⁴ Along the northeastern Pacific margin, both gastropods and bivalves show highest species richness in the tropics, with the number of species declining markedly with latitude (Figure 8.3). A tropical to

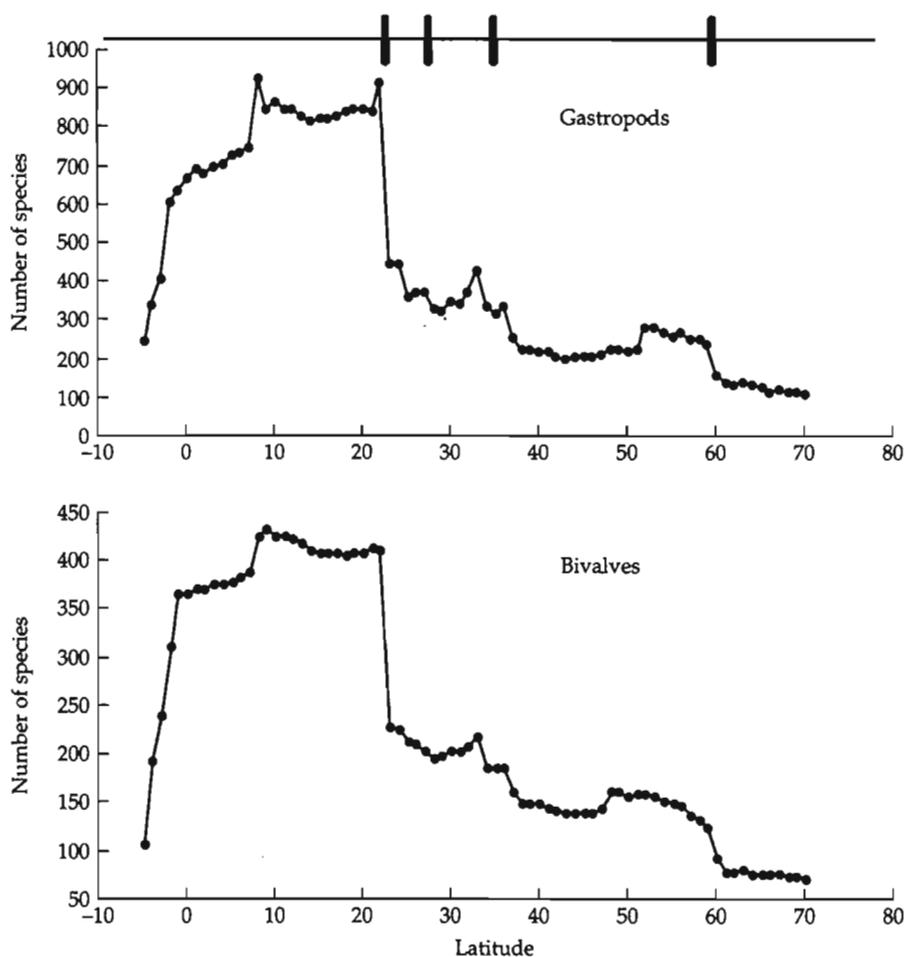


FIGURE 8.3 Latitudinal gradient in species richness of bivalves and gastropods along the northeastern Pacific continental shelf (depth <200 m). Vertical bars mark the position of the major biogeographic boundaries, defined by species range endpoints.

temperate decline in molluscan diversity is also evident in the Southern Hemisphere, but in this case with a modest reversal of the trend in southern Chile (Valdovinos et al. 2003; Marquet et al., this volume). Functionally, marine bivalves fall into two basic categories, depending on their life positions: infaunal species that burrow or bore into the substratum, and epifaunal species that live at the surface (Stanley 1988). The ratio of the number of infaunal to epifaunal species provides a very simple measure of how total richness is partitioned between these two functional groups. While the species richness of northeastern Pacific bivalves decreases by a factor of four from the tropics to the Arctic, the infauna/epifauna ratio increases along this gradient (Figure 8.4). Infaunal species thus account for a disproportionately larger fraction of total diversity at high latitudes. But such a decoupling between latitudinal trends in functional and taxonomic diversity may not

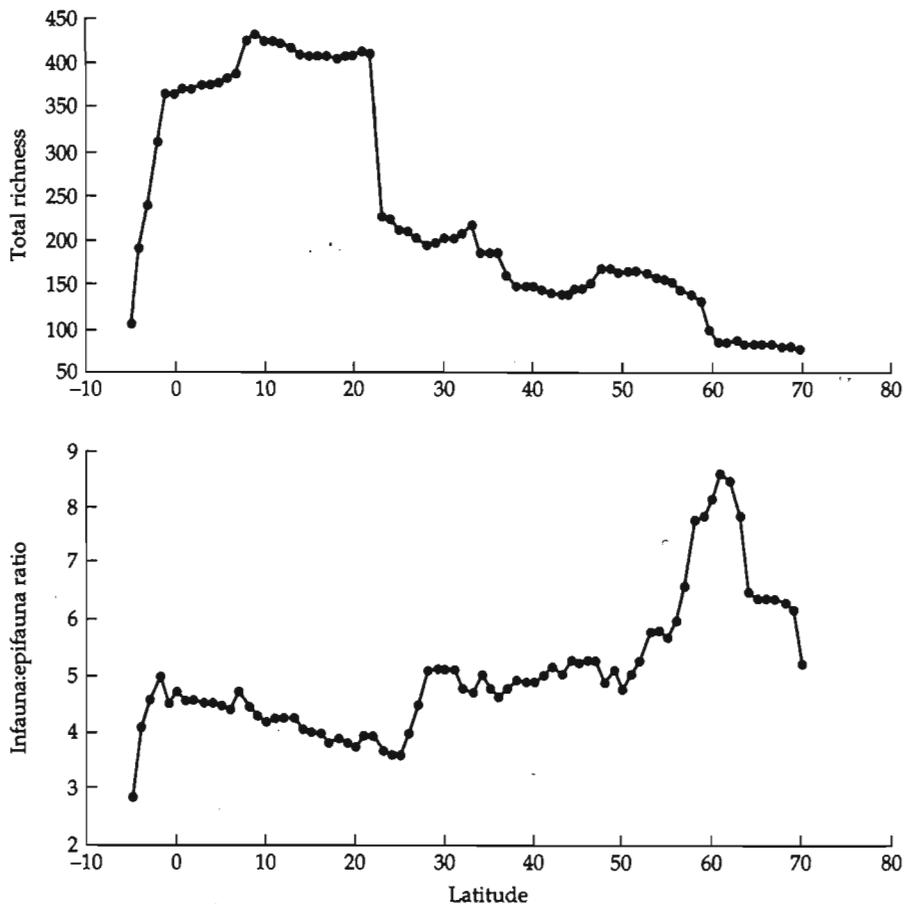


FIGURE 8.4 A comparison of latitudinal trends in species richness and infauna/epifauna ratio of northeastern Pacific marine bivalves. (After Roy et al. 2000.)

have always existed for bivalves. For example, late Jurassic (Tithonian stage, ~145–150 my BP) bivalves also had higher species richness in the tropics than in high latitudes, albeit with a shallower slope (Crame 2002). However, in contrast to today, the infauna/epifauna ratio decreased significantly with latitude during the Tithonian (Crame 1996), a trend that persisted at least until the latest Cretaceous (Jablonski et al. 2000). Thus the bivalves not only steepened their latitudinal diversity gradient over time, but also reversed the latitudinal trend in the proportion of their two primary functional groups. This reversal is probably related to the differential diversification of different clades along latitude (e.g., Crame 2002, and this volume), although the underlying mechanisms remain poorly understood. Without this functional perspective, the late Jurassic latitudinal diversity gradient simply looks like a damped version of the present-day trend in taxonomic richness, although in reality it had a fundamentally different functional makeup.

Bivalves are not the only group where spatial patterns of species richness fail to capture patterns of functional diversity. Gastropods show the expected strong latitudinal gradient in species richness along the northeastern Pacific coast (Roy et al. 1998), but as shown in Figure 8.5, this pattern is decoupled from the latitudinal trend in the ratio of carnivorous to non-carnivorous (C/NC) gastropods (Valentine et al. 2002). The latter is distinctly non-linear, with lowest values in the mid-latitudes and areas of highest and lowest species richness exhibiting comparable C/NC ratios. This trend in functional diversity is sensitive to the spatial scale over which it is calculated; the decline in C/NC ratio from the tropics to the temperate regions seen in Figure 8.5 essentially disappears at the provincial level (2.1 versus 1.9) even though species richness declines by 20% from 1386 to 1109. As in the case of bivalves, processes driving the spatial patterns of functional diversity in gastropods remain unknown, although the scale-dependence of the pattern suggests that the proximate cause is the differential spatial turnover of the species within the two functional groups (Valentine et al. 2002; Jablonski et al. 2003). Still unclear is whether such differences in distributional patterns reflect ecological controls or historical contingencies such as differential extinctions and/or range shifts in response to late Neogene environmental changes (Roy, Jablonski, and Valentine 2001; Todd et al. 2002).

The latitudinal trend in the C/NC ratio seen in northeastern Pacific gastropods may not be unique to that coast. Taylor and Taylor (1977) documented a qualitatively similar latitudinal trend for northeastern Atlantic gastropods. On the other hand, even though the latitudinal trend in species richness of gastropods along the northwestern Atlantic coast is remarkably similar to that along the northeastern Pacific coast (Roy et al. 1998), the C/NC ratios along those two coasts are markedly different (Roy, Jablonski, and Valentine, unpublished). Data for non-marine groups also show herbivore–carnivore relationships different from that in Figure 8.5 (Gaston et al. 1992; Van Valkenburgh and Janis 1993; Rosenzweig 1995). Clearly, there is a great deal of variation, mostly unknown, in the biogeography of functional groups.

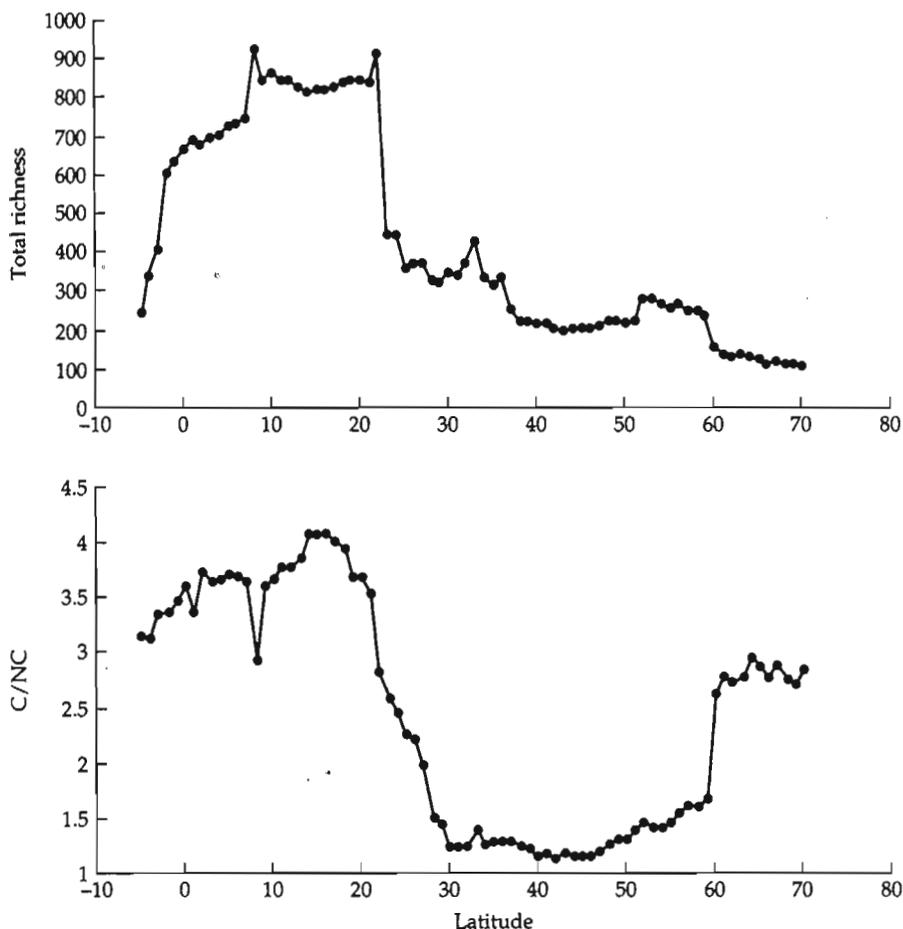


FIGURE 8.5 Comparison of latitudinal trends in species richness and carnivore/non-carnivore ratio (C/NC) of northeastern Pacific marine gastropods. (After Valentine et al. 2002.)

Provinciality and Biogeographic Boundaries

Climatic and oceanographic variables are among the most important forces structuring biogeographic patterns. In some regions, environmental conditions vary abruptly over short distances, whereas in other regions, various aspects of the environment change only gradually over long distances. The effects of such patterns of geographic variation on species distributions and therefore on biotic compositions are well known, ranging from relatively low levels of species turnover in regions of gradual change, to high levels of turnover among many groups in regions of abrupt change. The greatest biotic changes usually correlate with the boundaries of climatic zones and with altitude on land, and depth in the sea. As our experience has been chiefly with marine systems, we draw our examples from the oceanic realm.

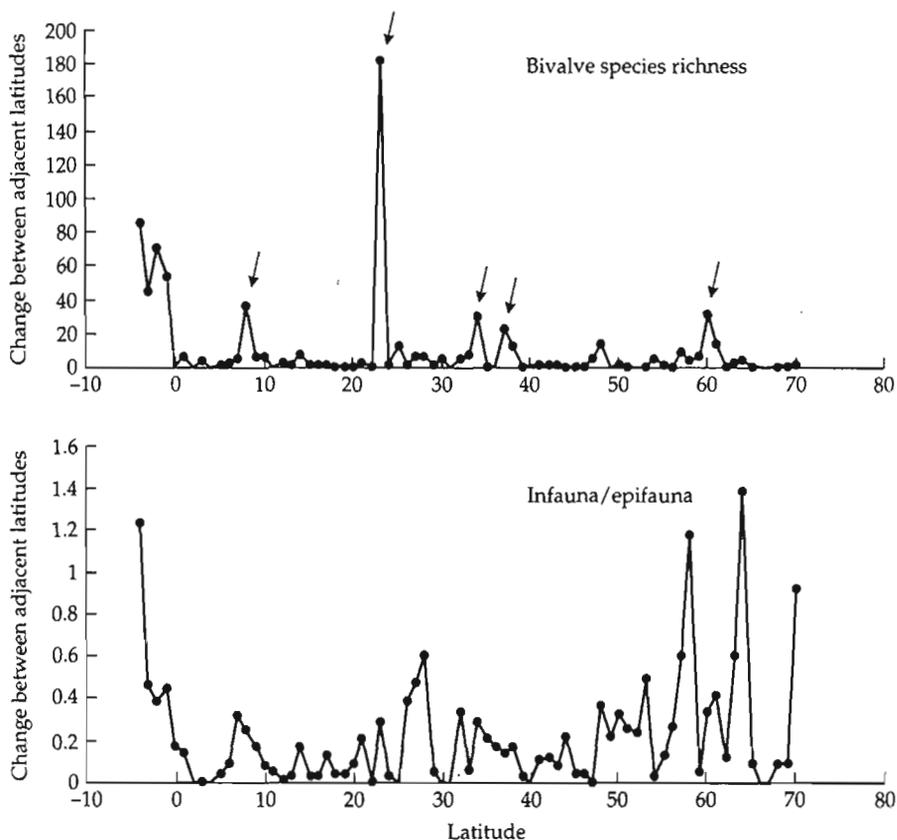


FIGURE 8.6 Spatial pattern of turnover of species richness and functional diversity in northeastern Pacific bivalves. Each point in the upper panel represents the total change in species richness between adjacent one-degree latitudinal bins. Arrows mark the position of major biogeographic breaks representing areas of high species turnover. Each point in the lower panel represents the changes in infauna/epifauna ratio along the same transect. Note the poor correspondence between the two patterns.

The more striking biotic effects of variations in environmental conditions are seen in patterns of provinciality, producing slightly—to distinctively different—faunas along geographic gradients. Provinciality, in the sense of magnitude of faunal turnover, is usually assessed by taxonomic criteria, although as indicated in previous examples, functional criteria are more likely to offer insights into the causal processes. At present, most continental shelves run north and south, crossing climate zones and isotherms, and thus many shelves display north-south chains of biodistributional regions. These regions are particularly well known for molluscs; one of the best-studied regions is the northeastern Pacific continental shelf. Figures 8.3 and 8.6 show a scheme for the main biodistributional regions of this continental shelf, based on molluscan species.

When evaluated in one-degree latitudinal bins, turnover among species of the shelled molluscan fauna of the northeastern Pacific shelf occurs in every bin, with a number of localized peaks (see Figure 8.6; Valentine 1966; Roy et al. 1994, 1998). The locations of high turnover have been taken as the boundaries of formally defined biotic provinces or sub-provinces (see Hall 1964 and Valentine 1966 for reviews); they tend to occur at regions of climatic zonal boundaries. Proceeding offshore, the provincial boundaries that have been studied are recognizable down to depths approximating the outer shelf edge, usually in the region of the thermocline, where the shelf fauna gives way to the cooler- and deeper-water fauna of the continental slope (Jablonski and Valentine 1981). Because temperature change is thus a major correlate of faunal change both latitudinally and bathymetrically, it has usually been considered as the major cause of provinciality, beginning as early as a chart by Dana (1853) and the remarkable biogeographic map by Forbes in Johnston (1856).

However, biodistributional boundaries—peaks in species turnover—also occur in places where local hydrographic conditions, rather than temperature, change abruptly. For example, Gaylord and Gaines (2000) have explored the possibility that a provincial boundary around Point Conception, California (near 34°30'N) is due to transport of larvae in a semi-permanent offshore current, thus blocking the dispersal of many species alongshore. They also note that some other biodistributional boundaries are also associated with offshore flows. The local hydrography also results in a temperature change in the area of Point Conception; however, the relative contribution of these two factors to this biogeographic break is not known. Finally, factors other than temperature and oceanography, such as habitat failure owing to deep-water channels or basins that interrupt shallow-water habitats, can also lead to localized turnover in species that can be recognized as a biogeographic boundary.

Clearly, biodistributional units defined from species compositions are of great biogeographic interest, and they may differ by more than one criterion. Factors such as range end-point frequency, level of endemism, taxonomic richness, physical nature of the boundary, and so forth are all useful in defining and evaluating biogeographic units. But a question that has not been much explored is whether functional and morphological diversity patterns also show provincialization, and, if so, whether those divisions coincide with units based on taxonomic criteria. The northeastern Pacific molluscan examples discussed above show that changes in functional diversity are not necessarily concentrated at provincial boundaries marked by clustering of species range endpoints (see Figure 8.6). Thus, a different biogeographic pattern emerges for functional diversity of these molluscs. Similarly, latitudinal patterns of body size of bivalves along the northeastern Pacific coast provide an opportunity to address the effects of provinciality on that important aspect of morphological diversity (Roy, Jablonski, and Martien 2000; Roy and Martien 2001). Surprisingly, at the provincial level the overall size-frequency distribu-

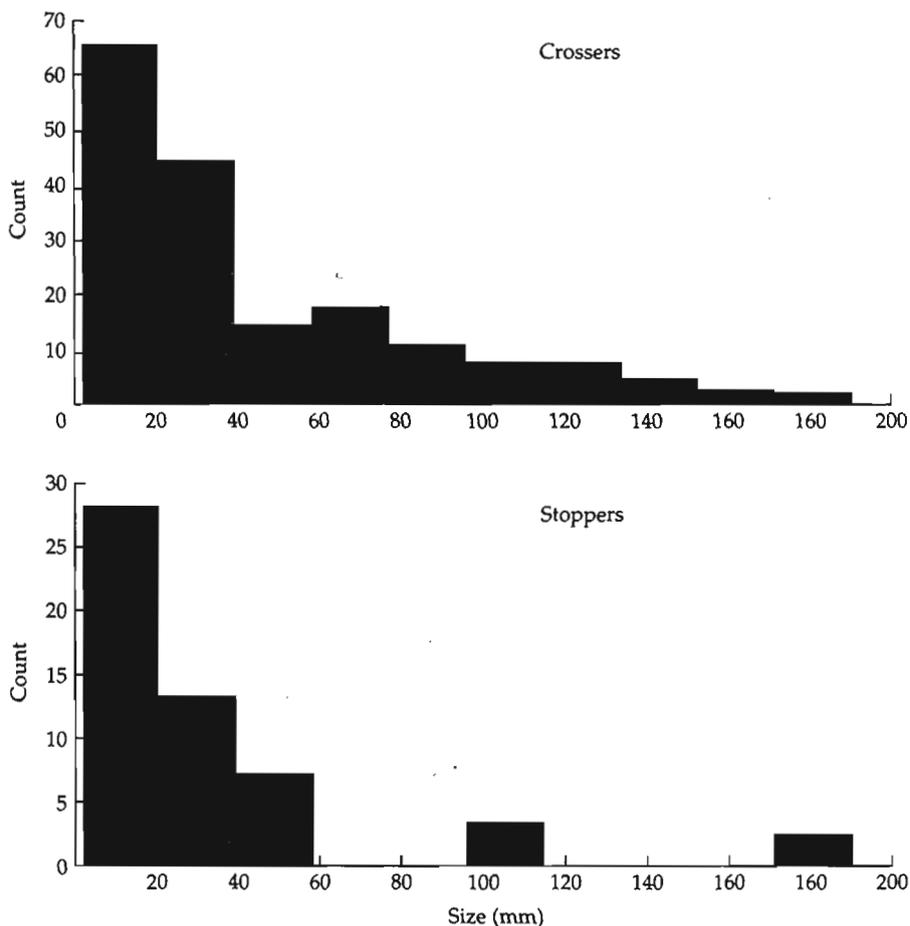


FIGURE 8.7 Body sizes of northeastern Pacific bivalve species across Point Conception, California, a major biogeographic boundary. The top panel shows the size frequency distribution (SFD) of species whose latitudinal ranges span this boundary ($N = 177$). The bottom panel shows the SFD of species whose range endpoints are at Point Conception ($N = 56$). Size is measured as the geometric mean of length and width (see Roy, Jablonski, and Martien 2000). The two distributions are significantly different ($p = 0.02$, Kolmogorov-Smirnov test) and the species ending their ranges at this boundary are smaller (median size 17 mm versus 30 mm).

tion is statistically indistinguishable from the tropics to the arctic, suggesting that provinciality has little effect on regional patterns of body size distributions. Even more remarkably, this similarity exists despite the fact that provincial boundaries show significantly more change in body size than do latitudinal bins away from a boundary (Roy and Martien 2001). In addition, some of the provincial boundaries such as the Californian-Oregonian province boundary (warm- to cool-temperate) are size-selective, with larger-bodied species crossing preferentially (Figure 8.7). Thus the rather monotonous intraprovin-

cial bivalve size frequencies are perturbed at provincial boundaries but are restored within the provinces, implying a replacement of species in size classes that are depleted at the boundary. While this suggests convergent body size evolution between provinces, the underlying evolutionary dynamics remain unknown.

Testing Hypotheses about Diversity Dynamics

Functional Groups and Species-Energy Relationships

Among the hypotheses proposed to explain the latitudinal diversity gradient, the species-energy hypothesis has attracted considerable interest (see Turner and Hawkins, this volume; Whittaker, this volume). This relatively simple hypothesis posits that the latitudinal gradient in species richness is primarily a function of energy availability, with species richness of a region positively related to solar energy input (Wright 1983; Wright et al. 1993; Fraser and Currie 1996; Kerr and Packer 1997). Thus, a positive correlation between some measure of energy and species richness is generally taken as supporting this hypothesis (Fraser and Currie 1996; Kerr and Packer 1997; Roy, Jablonski, and Martien 2000; Francis and Currie 2003). However, the actual mechanisms relating available energy to species richness remain largely unknown (Gaston 2000), so that specific predictions regarding, for example, the slope of the species-energy relationship have been lacking. Energy can be regarded either as an element in trophic dynamics, in which case it is related to the regime of productivity that includes solar radiation and nutrient supply (Valentine 1983), or as generating diversity patterns through metabolic scaling relationships, in which case it is related to temperature *per se* (Allen et al. 2002). While a positive relationship between energy and species richness is known in groups ranging from terrestrial trees and mammals to marine molluscs and reef corals (Wright 1983; Wright et al. 1993; Fraser and Currie 1996; Kerr and Packer 1997; Roy, Jablonski, and Martien 2000; Francis and Currie 2003), the differences in the slopes of the relationship from one group to another have been difficult to interpret. However, a recent theoretical model argues that temperature regulates species richness primarily through the biochemical kinetics of metabolism. This provides a quantitative prediction of how species richness should increase with environmental temperature (Allen et al. 2002). In particular, this model predicts that (1) the natural log of species richness should be a linear function of $1000/T_{\text{env}}$, and (2) the slope should approximate -9.0 Kelvin (K) (Allen et al. 2002). These predictions allow us to test quantitatively how different functional groups respond to the same changes of available energy along a latitudinal gradient.

For benthic marine invertebrates, mean sea surface temperature (SST) provides a good approximation of available solar energy. Previous studies have revealed a significant positive relationship between the latitudinal gradient

in mean SST and total species richness for both gastropods and bivalves (Roy, Jablonski, and Valentine 2000). However, when these latitudinal trends are partitioned into different functional groups, interesting differences emerge. Gastropods along the northeastern Pacific and northwestern Atlantic coasts exhibit an average slope of approximately -7 K, quite close to the model prediction (Allen et al. 2002). In the northwestern Atlantic, both carnivorous and non-carnivorous gastropods exhibit slopes that are very similar to the overall slope, as do the northeastern Pacific carnivores (Figure 8.8). However, the slope for the non-carnivorous northeastern Pacific gastropods is significantly lower (-2.7 K). Clearly, the latitudinal diversity trend of this latter functional group cannot be explained by the biochemical kinetics model, even though the general prediction of the species-energy theory (i.e., a positive relationship between temperature and species richness) is supported. In addition, while richness is a fairly continuous, linear function of energy input for the eastern Pacific, the western Atlantic patterns are strongly non-linear, with cold-temperate and boreal assemblages of both carnivorous and non-carnivorous gastropods deviating from the predicted slope (see Figure 8.8). Finally, the overall slope for northeastern Pacific bivalves is significantly lower than that of the gastropods and the model's prediction, and within bivalves, the infaunal species exhibit a slope significantly lower than epifaunal species (Figure 8.9).

The differences in the slopes of the temperature-richness relationship between different functional groups raise interesting questions regarding the dynamics of diversity, and help put the discordances between latitudinal patterns of functional diversity and species richness into perspective. Although bivalves do not conform to the relationship found in many other groups, both terrestrial and marine (Allen et al. 2002), they show significant differences related to life habits. Similarly, the non-carnivorous gastropods along the northeastern Pacific are clearly different from carnivorous species along the same coast and from non-carnivorous species along the northwestern Atlantic coast. These differences could stem from historical factors or ecological ones. For example, the deviations could reflect nonequilibrium conditions such as the lack of rebound from selective extinctions during the late Neogene. Alternatively, the deviations may reflect situations where the assumptions of the Allen et al. model, such as a linear relationship between environmental temperature and population density, are violated. Both of these hypotheses are testable using paleontological and ecological data, and the gastropod contrasts are not as surprising when we recall the contrast in C/NC ratio patterns along the east and west coasts of the Americas. Such tests are clearly needed to better understand the dynamics of diversity along latitudinal gradients. In general, these examples also show that tests of species-energy and other hypotheses, using total species richness values, are only crude tests at best; incorporating information about life habits of species reveals patterns previously not detected.

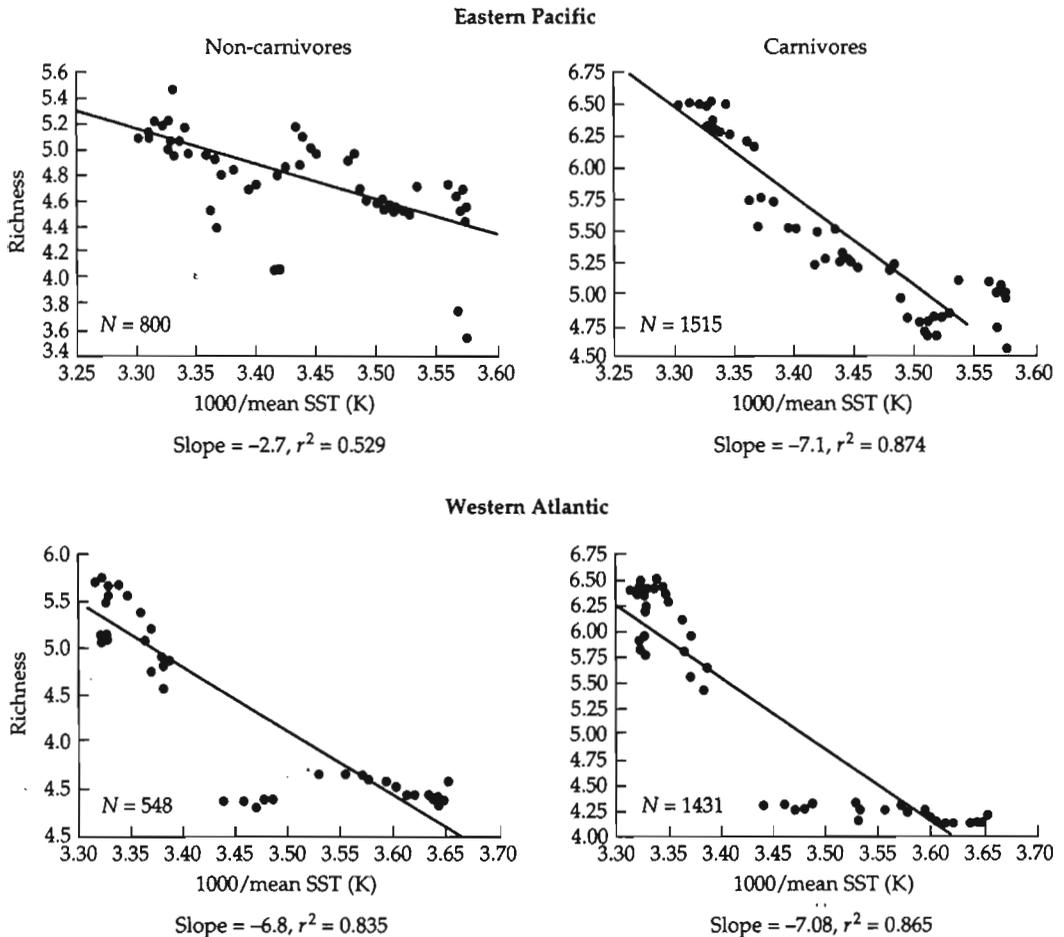


FIGURE 8.8 Test of the relationship between species richness and temperature in marine gastropods along the northeastern Pacific and northwestern Atlantic coasts following Allen et al. (2002). Temperature is defined as $1000/\text{mean SST}$ in Kelvins. The slope of the northeastern Pacific non-carnivorous species is significantly different from the others; see text for details. Species richness and temperature data from Roy et al. 1998.

EXTINCTION SELECTIVITY. Many authors have recognized that the loss of biodiversity involves not only the disappearance of taxa, but of functional groups and morphological variety as well. However, the role of extinction in shaping spatial patterns of biodiversity—functional, morphological, or taxonomic—is poorly known. During the major mass extinctions in the geologic past, one of the most pervasive predictors of genus survivorship was geographic extent (Jablonski 1995), which of course may or may not correlate

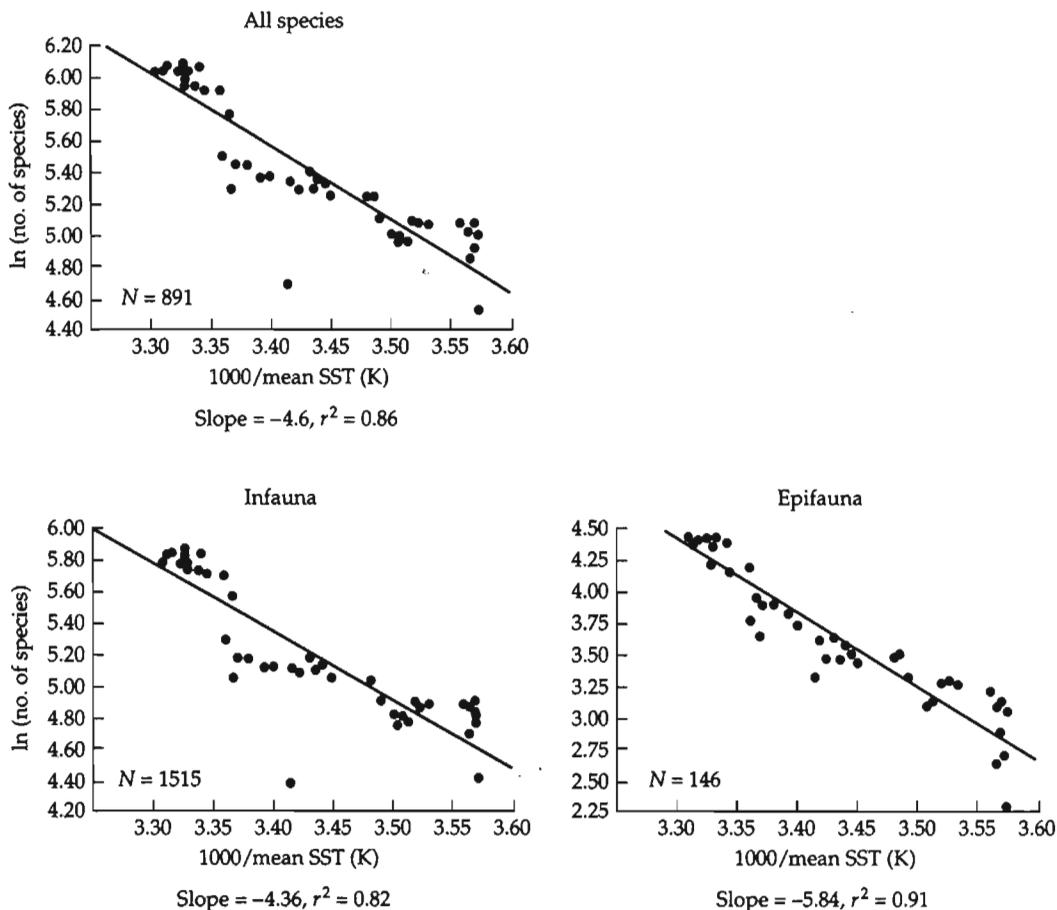


FIGURE 8.9 Same relationship as in Figure 8.8, but for northeastern Pacific bivalves. The overall slope for bivalves is significantly lower than that of gastropods and that predicted by the Allen et al. model. Furthermore, the slopes for the infaunal and epifaunal species are significantly different; see text for details.

with, and thereby promote, other aspects of form or ecology (see also Raup and Jablonski 1993). Thus, the end-Cretaceous mass extinction favors widespread clades but is non-selective with respect to molluscan functional groups, body size, abundance, and many aspects of morphology (Jablonski and Raup 1995; Jablonski 1996; Harries 1999; Lockwood 2003). When other aspects of ecology correlate with geographic distribution, separating true selectivity from hitchhiking effects is difficult. For example, the end-Ordovician extinction apparently selected against high levels of colony complexity or integration in Paleozoic bryozoans, but these factors also correlate inversely with geographic distribution (Anstey 1978, 1986); moreover, among Paleozoic brachiopods extinction selects against “more specialized and higher adaptive morphs having more restricted distributions” (Harper and Rong

2001). Similarly, major extinctions repeatedly removed the most complex forms of planktonic foraminifera. But was the decisive factor morphological complexity, or their narrower geographic distribution? Was it their more specialized position in the water column, or their reproductive ecology? Or, was it a preferred tropical climate zone compared to more widespread, generalist forms (see Norris 1991, 2002)? Such potential covariation also emerges when apparent extinction hotspots tend to coincide with regions particularly rich in endemic genera (Jablonski 1995: 35, and references therein). Extinction selectivities on biotic factors such as body size, abundance, or life habits are actually most pronounced in times of milder extinction intensities than those estimated for the "Big Five" mass extinctions (e.g., in the geologic past, Jablonski 1995; McKinney 1997; Kammer et al. 1998; Smith 2000; in present-day biotas, Gaston and Blackburn 1995; Bennett and Owens 1997; McKinney 1997; Purvis et al. 2000; Cardillo and Bromham 2001; von Euler 2001).

When extinction is truly random, we expect only modest declines in functional or morphological diversity even when a substantial number of species are lost (Foote 1997; Nee and May 1997), although the interaction of low diversity and intense extinction can drastically reduce morphological variety owing to sampling error (e.g., Foote 1996, 1997). Contrary to this expectation, the few analyses performed thus far have found that, even when taxonomic richness is relatively high, morphological variety tends to be truncated rather than thinned during mass extinctions (e.g., Roy 1996; Lockwood 1998; McGhee 1999; see also Petchey and Gaston 2002). But these non-random patterns need not map onto conventional taxonomic or functional groupings. For example, end-Permian and Triassic ammonoid extinctions are not selective with respect to the basic morphotypes within the clade, but tend to leave survivors around the periphery of a multivariate morphospace, which is then filled in again during the evolutionary recovery phase (A. McGowan, pers. comm.). Such vacant portions of morphospace imply some kind of selectivity despite the lack of strong patterns in some of the most obvious morphological or ecological aspects of the victims and survivors; again geography may be crucial here, although we cannot rule out the many ecological factors that remain to be analyzed. Similarly, the loss of phylogenetic diversity (i.e., extinction of higher taxa or total phylogenetic branch length; Purvis et al. 2000) can be greater or less than expected from simple taxonomic extinction intensities depending on the degree and pattern of extinction selectivity: even substantial but random losses will leave phylogenetic diversity relatively intact, whereas more selective extinction can disproportionately reduce phylogenetic diversity (Nee and May 1997; Purvis et al. 2000; von Euler 2001).

Evolutionary and ecological recoveries may be as important in shaping the post-extinction biota as the extinction events themselves (e.g., Erwin 2001; Jablonski 2001, 2002), but here we have even fewer spatially explicit data than for the extinctions themselves. Jablonski (1998) found significant interprovincial differences in the recovery of marine molluscan faunas after the end-Cretaceous (K/T) mass extinctions, but this was strictly a taxonomic analysis

and did not address morphological or functional aspects of those faunas (and see Rees 2002 on regional patterns in Permo-Triassic floras). A morphological extension of the differences in K/T recovery dynamics would be worthwhile, particularly because those differences were accompanied by interprovincial variations in the intensity of post-extinction invasions—important for present-day biodiversity—and the invaders were not randomly drawn from the pre-extinction biota (Jablonski 1998). In apparent contrast, although ammonoid cephalopods undergo spectacular episodes of taxonomic loss and recovery (e.g., at the end-Permian and end-Triassic mass extinctions), they show relatively little spatial patterning in their taxonomic and morphological recoveries (Dommergues et al. 2002). This lack of spatial structuring might have been expected from the wide distributions of many ammonoid species and clades and the general absence of a link between their shell morphology and biogeography; more analyses are needed in less vagile groups.

We still do not know the role of selective extinction or recovery during the Neogene or earlier times in sculpting the spatial patterns in functional or morphological diversity seen today. Regional variations in taxonomic extinction intensity have been reported (e.g., Stanley 1986; Todd et al. 2002), but their larger and long-term biotic effects remain poorly known. In the best-studied example, differential extinction and diversification among molluscan functional groups following the uplift of the Panamanian Isthmus drove divergent biotic changes in the tropical Atlantic and Pacific faunas from what had been a single trans-isthmian biota (Todd et al. 2002), and we suspect that comparable differences in extinction and recovery dynamics will prove to be pervasive in the face of the provincialization of the Neogene world as polar refrigeration set in. What is astonishing about the suite of functional divergences in this case is the near-identical taxonomic diversities attained by the two faunas despite their differences in extinction intensities and the differential recovery of disparate functional groups (see Roy et al. 1998).

Present-day extinction risk is clearly not distributed evenly over the globe, as attested by many regional risk assessments and hot-spot analyses. The impact of regional losses in taxonomic richness on the functional or morphological diversity is only now being addressed, however. In a pioneering study, Jernvall and Wright (1998) showed that the expected ecological or functional losses owing to impending taxonomic extinctions in primates differed among regions depending on their respective morphospace occupation patterns and thus were not predictable from taxonomic data alone. Whether this is a common pattern remains to be determined.

Frontiers of Biodiversity Dynamics

A resurgence of interest in biogeography and macroecology combined with wide availability of digital databases is producing increasingly refined data on species distributions, both past and present. These data are being used to test traditional as well as new hypotheses about processes regulating spatial

patterns of diversity. However, the vast majority of studies that quantify biogeographic patterns and address macroecological hypotheses to explain those patterns still rely on counts of species or higher taxa. Yet as we discussed above, taxonomic patterns are only one aspect of biodiversity and may often mask interesting spatial patterns of morphological, functional, or phylogenetic diversity. In macroecology, the search for correlations between present-day patterns of species richness and environmental or biotic variables has so far largely ignored the role of functional biology and ecology of individual species or lineages, and hence has limited ability to inform us about the processes actually underlying those correlations.

For example, the species-energy hypothesis for latitudinal and other diversity trends has almost always been tested in terms of correlations of species richness and various energy-related variables. But species' energy use is determined by their functional biology, and differences in energy use should translate into predictable trends in spatial patterns of other aspects of diversity such as body size (Cousins 1989; Turner and Lennon 1989; Cushman et al. 1993; Blackburn and Gaston 1996; Roy and Martien 2001). At least some groups that show a significant positive correlation between taxonomic richness and energy, such as marine bivalves (Roy et al. 2000), fail to exhibit spatial patterns of body size predicted from energy availability (Roy and Martien 2001). Similarly, while marine bivalves and gastropods in the Northern Hemisphere show an overall positive correlation between species richness and energy, the slope of this relationship varies significantly among functional groups. These differences could derive from fundamental differences in macroecological relationships (e.g., relationships between environmental temperature and population density) that reflect differences in the biology of different functional groups, or from historical effects such as differential extinction or recovery during the late Neogene. All of this suggests that general correlations between species richness and energy variables provide, at best, a crude insight into the dynamics of diversity and can mask deviations from expectations that may ultimately be more revealing of underlying mechanisms. Understanding the causes of these deviations is ultimately the key to understanding the processes that relate available energy to biodiversity patterns.

Finally, the role of historical processes in generating present-day species diversity patterns remains seriously understudied. The increasing use of phylogenetic relationships to evaluate the role of historical factors is encouraging in this respect, but a major problem in relying on phylogenies of living species is that it ignores the role of selective extinctions. Yet, there is increasing evidence that extinction events outside of major mass extinctions tend to show selectivities with respect to morphology, ecology, geography, or phylogenetic affinities. Even the "Big Five" extinction events of the geologic past are not entirely random with respect to biodistributional factors. Understanding the role of extinctions during the recent geological past in shaping present-day biodiversity patterns remains a major challenge for biogeography and macroecology. Addressing this would require us to better quantify Neogene extinc-

tion patterns for groups with a good fossil record, and to generate better models for how selective extinctions affect topologies of phylogenetic trees; the latter may be the only solution for poorly fossilized groups.

Despite major conceptual advances and the availability of large amounts of data, our knowledge of biogeographic patterns still rests on species counts. Further refinements of such spatial distributional data are undoubtedly important and should be encouraged. However, in our view, a true understanding of the processes underlying diversity patterns requires better information on other aspects of organismal biology and geographic variation in these characters. Incorporating information on morphology, functional biology, and phylogenetic affinities of species in biogeographic databases is not only technologically feasible, but a necessity. Such data would finally produce a biogeography that is truly reflective of the variety of life.

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