

MATTERS OF THE RECORD

Incumbency, diversity, and latitudinal gradients

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Physical environmental factors have been seen as paramount in determining many large-scale biodistributional patterns in time and space. Although this is probably correct for many situations, this view has become so pervasive that it has led to the neglect of the role of biotic interactions in setting large-scale diversity patterns. (In this paper diversity denotes taxonomic richness.) New approaches to this perennial debate on the roles of physical and biotic forces in paleoecology and macroevolution are needed, and here we explore an argument for the role of incumbency or priority effects in the dynamics behind the most dramatic spatial pattern in biodiversity, the latitudinal diversity gradient.

A global analysis of the fossil record of living marine bivalve genera and subgenera (hereafter simply genera) of the continental shelves provides perhaps the strongest evidence for the Out of the Tropics (OTT) dynamic associated with the formation of the present marine latitudinal diversity gradient (LDG) (Jablonski et al. 2006). The marine LDG appears to be driven primarily by the origin of novel lineages in the Tropics, some of which then expand their ranges into higher, extratropical latitudes (see Jablonski 1993, 2005; Clark and Crame 2003; Goldberg et al. 2005; Jablonski et al. 2006; Martin et al. 2007). Support for this pattern comes from the overwhelmingly tropical first fossil occurrences of living bivalve genera and their subsequent appearances in higher latitudes. Some genera are first found in the extratropical fossil record, but these never match, at any latitude, the

number or proportion of genera that have expanded from the Tropics (the ratio is generally ~3:1), and even this smaller number is probably an overestimate, because the extratropical post-Paleozoic fossil record is so much better sampled than that of the Tropics (Allison and Briggs 1993; Jablonski 1993; Jackson and Johnson 2001; Jablonski et al. 2006; Valentine et al. 2006). The result is a gradient wherein the majority of taxa in each latitudinal bin is shared with the Tropics. For genera that originate extratropically, expansion into the Tropics is virtually unknown, at least at shelf depths, and given the anti-tropical bias in the evidence of first occurrences, most apparent instances may be artifacts (Jablonski et al. 2006; see also Vermeij 2005a). Over the past few centuries, successful species invasions have been less frequent in tropical than extratropical regions, at least for mainland terrestrial communities, even though several studies have shown a positive relationship between the number of exotic and native species within climatic zones (Rejmánek 1996; Sax 2001; Fine 2002; Sax and Gaines 2006; Fridley et al. 2007). Fewer data are available for marine tropical settings, but success rates of invasions from the temperate zones also appear to be low, outside of severely disturbed or novel habitats (e.g., Hewitt 2002; Paulay et al. 2002; Fridley et al. 2007). Here we explore some features that may regulate this evolutionary and biogeographic dynamic, and advance a counterintuitive hypothesis in hopes of stimulating research into the neglected role of biotic factors in shaping the LDG.

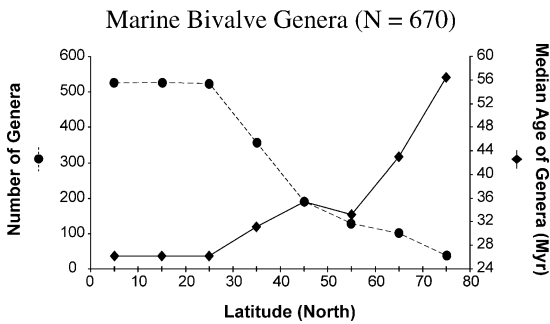


FIGURE 1. The median ages of living marine bivalve genera (solid line, diamonds) increases with latitude as the number of genera (dashed lines) decreases. Modified with added data from supporting online material in Jablonski et al. 2006.

Related to the OTT dynamic is the increase in median ages of bivalve genera with latitude as the number of genera decreases (Fig. 1). The tropical fauna retains most of the older genera as they expand, but its high origination rate imparts a younger average age to the fauna there (see Foote 2001 on the dynamical interpretation of taxon ages). This interpretation is supported by Crame's (2000) observation that diversity gradients are steepest for the bivalve clades dominated by younger genera. The few genera residing in higher latitudes are thus biased toward those that evolved earliest, many demonstrably at low latitudes (Jablonski et al. 2006). Even the few groups with peak diversity outside the Tropics, such as the anomalodesmatan bivalves, share the same fundamental relationship between taxon age and diversity, with minimum genus ages roughly coinciding with their extratropical diversity maxima, and age maxima coinciding with diversity minima (Krug et al. 2006 and unpublished data). In theory, patterns of species-level origination might differ from those of lineage formation at the genus level. Unfortunately,

ly, a definitive global data set of the ages of marine bivalve species is not available. However, because only one species need reach higher latitudes to create a record of its genus there, these categories are linked to some extent. High-latitude species might be older than tropical ones, although active recent high-latitude speciation is known or inferred in several terrestrial groups (see Mittelbach et al. 2007 and Wier and Schluter 2007 for references). However, the species/genus ratio is low for extant high-latitude bivalves globally (Polar S/G: 1.9; Tropical S/G: 5.1, suggesting sluggish per-taxon rates of marine speciation in polar regions [Krug et al. 2008]).

Possible Causes of Latitudinal Diversity Dynamics

The genus-level diversity gradient must be explained by some combination of origination, extinction, and dispersal rates, and recent models have explored interactions among these parameters (see Roy and Goldberg 2007). As noted above, origination rates are highest in the more diverse regions and taxa are exported to higher latitudes without erasing latitudinal diversity trends, so either there is a gradient in extinction or young genera are being prevented from dispersing, or both. As shown below, paleontological estimates of generic extinction rates in the Pliocene and Pleistocene (~0.012–5 Myr ago) are no higher (and may be lower) in polar regions than in temperate latitudes, so differential extinction alone cannot account for the temperate to polar decline in diversity (we use polar here simply to denote regions poleward of 60° latitude). Thus one or more factors not directly related to origination and extinction rates per se must impede the cross-latitudinal expan-

TABLE 1. The qualitative pattern of factors associated with an incumbency model that proposes a filtering of the poleward spread of lineages, chiefly arising in the Tropics, to shape the latitudinal diversity gradient. Factors 1 to 4 are based on observations whereas factors 5 and 6 are inferential.

Factor	Tropical zone	Temperate zone	Polar zone
1. Diversity	High	Intermediate	Low
2. Median age of genera	Low	Intermediate	High
3. In-situ origination rate	High	Low	Low
4. Extinction rate	Low	Higher?	Low
5. Invasibility	Low	Higher?	Low
6. Niche breadth	Narrow	Intermediate	Broad

sion of lower-latitude genera through restrictions on their contained species. These potential constraints fall into three general categories.

1. *Time*.—Many genera show a latitudinal array of species along shelves, with poleward spread presumably involving speciation across latitudes. Perhaps, then, insufficient time has elapsed for the accumulation of poleward speciations in many lineages. “Age and area” arguments, with geographic expansion as a positive function of taxon age, have a long pedigree (e.g., Willis 1922; Miller 1997; Jones et al. 2005; see Mittelbach et al. 2007 for a review). However, the LDG has been at least a semi-permanent feature of the marine biosphere for much of the geologic past and seems to have been present in something like its current form not just in the Neogene, but since the Mesozoic breakup of Pangaea (Crame 2001, 2002), though evidently with a lower slope during nonglacial intervals. Given that even complete polar extinction (e.g., during glacial episodes, an improbable event for subtidal organisms) would leave a pool of potential invaders in adjoining provinces (e.g., Hickerson and Cunningham 2006), expectations for a time frame within which to measure the lag for spreading into high latitudes are uncertain. Today’s Arctic Ocean first became a fully marine feature nearly 17.5 Myr ago, shortly before the time of peak mid-Miocene warming (Jakobsson et al. 2007), when temperate latitudes harbored a relatively rich bivalve fauna (e.g., Gladenkov and Sinelnikova 1990; Ward 1992; Ogasawara 1994). Both dispersal and local adaptation can be rapid relative to the time available.

2. *Abiotic Aspects of Environmental Harshness or Invasibility*.—Many authors have suggested that the harsher climate encountered in higher latitudes produces physiological barriers that exclude most lineages (see review by Willig et al. 2003). In this view, only a few lineages can adapt to conditions at very high latitudes, but those that do so may diversify there. Temperature has been a prime suspect in regulating the LDG, and temperature correlates significantly with both bivalve and prosobranch gastropod diversity along north-south shelves (e.g., Roy et al. 1998, 2000). However, the ex-

istence of a diverse deep-sea fauna at low temperatures indicates that evolution is quite capable of overcoming physiological problems associated with the low end of the marine temperature range. The fact that most of the marine bivalve families absent from the deep sea are suspension feeders (Knudsen 1979; Gage and Tyler 1991; Valentine et al. 2006) suggests that the attenuation of trophic resources may be a more important barrier than low temperature (see Rex et al. 2005 for a similar argument for species richness in the abyssal environment). Furthermore, temperature variability does not correlate with the LDG, for it is greatest in middle and least at low and high latitudes (Valentine 1973). Air temperatures can certainly be very low in high latitudes, affecting intertidal forms, and intertidal and shallow subtidal zones may be ice covered or scoured, precluding living space seasonally. However, the bulk of the bivalve fauna can live subtidally, in environments with more stable though low temperatures. Even in the terrestrial realm, a quantitative assessment of factors affecting vascular plant diversity patterns did not find mean annual temperature per se to be an important contributor (Kreft and Jetz 2007). Regarding other physical variables, habitat area has also been implicated in terrestrial gradients (e.g., Rosenzweig 1995), but along the northeastern Pacific, shelves are broadest in higher latitudes, whereas the tropical shelf is quite narrow and embraces a relatively small area; habitat area thus opposes the LDG (Roy et al. 1998). Habitat heterogeneity seems important locally, but at least for regions that lack coral reefs, as in the eastern Pacific, the heterogeneity of physical habitats does not differ obviously between high- and low-latitude shelves. Area and heterogeneity differences may help to explain interregional diversity differences within climate zones, however (e.g., Crame and Rosen 2002; Rex et al. 2005).

3. *Biotic Aspects of Environmental Harshness or Invasibility*.—Such aspects would include food supply, activity of predators or pathogens, competition for space or specialized habitat resources, and more generally, ecological incumbency, priority, or niche preemption effects. Levels of primary productivity do not

strongly correlate with the LDG, either along the shelf or in the open ocean (Longhurst 1998); what correlation there is appears to be negative. *Variability* in productivity does seem to correlate well with diversity, owing chiefly to a significant latitudinal increase in seasonality (Valentine 1973, 1983; Valentine and Ayala 1978), but a gradient in seasonality of productivity cannot account for the gradient in the antiquity of generic lineages. However, the observed OTT dynamic, with depressed diversities and older faunas in progressively higher latitudes, would arise if the poleward faunas themselves have features related to seasonality and other latitudinally graded conditions that inhibit immigration.

Although each of these three types of factors might contribute to the present LDG, the third has garnered the least attention, so we focus here on evidence and interpretations that bear on the relation of faunal incumbency in biologically harsher or less receptive environments to invasibility. Much has been published on the tendency for incumbent taxa to depress the invasibility of a region, so that asymmetric biotic interchanges are often attributable to interregional variations in specialization, diversity and extinction intensity (e.g., Rosenzweig and McCord 1991; Vermeij 1991, 2005b; Jablonski and Sepkoski 1996; Beard 1998; Schluter 2000; Stachowicz and Tilman 2005; Wiens et al. 2006; Sax et al. 2007), but incumbency effects have rarely been invoked for the LDG.

Spreading Across Latitudes

If latitudinal variations exist in invasibility, the LDG could involve a source-and-filter process rather than simple diffusion. Movement of populations along a shelf can be accomplished by the spreading of populations along the more or less continuous shelf habitats, where long-distance transport is probably not required; the species are already present in the adjoining territory and short-range dispersals should usually suffice for invasion, provided that any former ecological barriers to their dispersal, such as at provincial boundaries, have ameliorated.

Arim et al. (2006) reviewed data on the spread of invaders and discuss the concept of

spread dependency, which is somewhat analogous to density dependency (Smith 1935) in population biology and to diversity dependency (Valentine 1972) in evolutionary paleoecology. Spreading rates recorded for an assortment of invaders suggest linear negative feedbacks that cause asymptotic approaches to an equilibrium spread rate. As Arim et al. note, this dynamic suggests the same kind of resource competition that limits population growth. However, spreading rates associated with global or regional warming, for example, might also be constrained by the rate of warming, or by some intrinsic limitation that might lag behind that rate. The geographic range limits reached by spreading species are presumably imposed by a mix of factors similar to those that constrained their ranges in their previous territories. To be sure, the spread of species across important barriers, as between widely separate habitat islands, requires a founding invasion and favors the better dispersers. However, the LDG for species of major constituents of western Pacific coral reef communities, which require long-distance founding events in many cases, is symmetrical around a low-latitude peak despite the uneven latitudinal distribution of reef-bearing shelves and island platforms (Roberts et al. 2002; Connolly et al. 2003).

Shifts in latitudinal ranges along shelves are best known during climate change, when warmer- or cooler-adapted species track isotherms. The most recent fossil records of poleward marine expansions are associated with the warming interglacial trends of the Pleistocene (e.g., Valentine 1961 for the Californian Province; Tankard 1975 for South Africa; Raffi et al. 1985 for the Mediterranean; Kendrick et al. 1991 for Western Australia; Kitamura et al. 2000 for Japan). When climates then cool, as during glacial intervals, some species' poleward limits retreat toward the equator, with species that have extended their ranges toward the poles during warming being the ones most likely to retreat equatorward during cooling (see Roy et al. 1995). The shape of the LDG thus may change during these climate swings, but commonly this is reversible; evidently some other step or condition is required for significant and permanent changes

to the latitudinal array of taxa across zonal climates. However, such short-term climate changes do provide a mechanism for introducing lineages, at least temporarily, into latitudes from which they had been absent.

Incumbency and Adaptation

If incumbent lineages preclude or at least inhibit invasions, diversity-dependent factors are presumably at work. Diversity-dependent factors are those arising from resource limitations; when conditions do not favor resource partitioning, diversity must be relatively low, whereas greater partitioning will accordingly permit diversity to be higher (Valentine 1972). Factors such as temperature that are not actually partitioned among individuals, populations, or taxa—factors that are not used up by organisms—are diversity-independent in this sense.

Diversity-dependent factors are inferred to be related to environmental heterogeneity, either spatial or temporal. The correlation of diversity with spatial habitat heterogeneity has been demonstrated by experiment or observation in ecological time, from the population up to the community level (e.g., Crombie 1945; Etter and Grassle 1992; Armbecht et al. 2004), and analyzed in evolutionary time at provincial and global levels (see Valentine 1973; Lomolino et al. 2006). As noted above, however, such variation cannot itself account for the LDG. The effects of temporal instability in productivity are likely to involve evolutionary rather than ecological scales and so are not amenable to experimentation, but as seasonality in productivity grades latitudinally it is a candidate for affecting the LDG. The hypothesis is that where trophic resource variability is high, species persist by maintaining large populations, and/or by inhabiting a wider range of habitats, and/or by consuming a wider range of food items, particularly items low in the trophic chain, relative to species in trophically stable environments (Valentine 1973, 1983; the latitudinal shift to nonfeeding larvae in higher latitudes documented by, e.g., Thorsen 1950; Jablonski and Lutz 1983, and Laptikhovskiy 2006, may also be part of an adaptive syndrome for increased seasonality, as this would buffer larval survival against

variability in trophic resource availability). Thus the average higher-latitude species is ecologically more generalized and requires a larger share of available resources than the average lower-latitude species. Furthermore, more trophic resources may escape the consumer portion of the food web when productivity is variable, producing lags between rises in productivity and increases in consumption. Therefore more resources are required to support the average species, and fewer species can be supported in trophically variable environments. This is a different view from approaches that hold lower species diversity to reflect open niches and greater resource availability (for review see Stachowicz and Tilman 2005) and from ideas that invoke a latitudinal gradient in environmental tolerances and therefore geographic ranges, as suggested by Rapoport's Rule (Stevens 1989; rejected for marine mollusks by Roy et al. 1994, and apparently not a general phenomenon; see Gaston et al. 1998; Ribas and Schoereder 2006; Ruggiero and Werenkraut 2007).

An incumbency hypothesis for the LDG requires that species living in high latitudes tend to be more generalized with respect to limiting resources than species living in low latitudes. This idea is supported by studies documenting narrower diets among tropical gastropods than in high-latitude forms, but the data are few (references in Valentine et al. 2002, and see Taylor and Taylor 1977, and also Sax et al. 2007 who propose that this notion may also apply in terrestrial systems). The observations that the range of morphological elaboration is greatest among tropical species (Vermeij 1978) may also be relevant here. This formulation implies a gradient of limits on local and regional carrying capacity. These limits presumably vary as environments change, and species may well be able to evolve strategies promoting denser ecospace packing than observed in the modern bivalve fauna. Nevertheless, the persistence of the LDG indicated by the fossil record suggests that the effects of incumbency that we hypothesize have been a general feature of faunal responses to latitudinal variation in diversity-dependent factors over long stretches of geologic time.

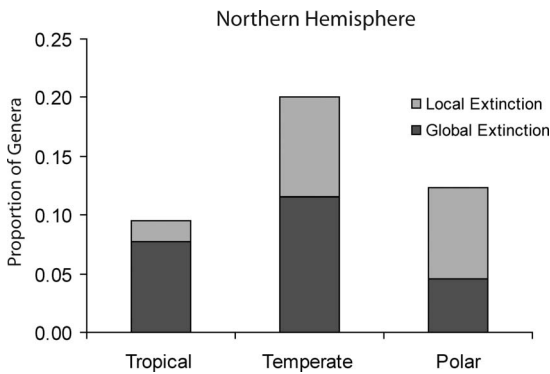


FIGURE 2. Preliminary estimates of local and global genus extinction intensity in tropical, north temperate, and north polar regions for the Pliocene and Pleistocene, based on augmented versions of the spatially explicit databases of living bivalve species and living and extinct bivalve genera described by Jablonski et al. (2006). Tropical local extinction estimated by the proportion of taxa originating in the Tropics in the late Miocene–Pleistocene that have lost their tropical presence (Jablonski et al. 2006). Tropical and temperate extinction intensities differ significantly ($p < 0.001$; log-likelihood ratio test); temperate and polar extinction intensities are not significantly different, as expected given lower polar n , but differ in predicted direction; polar intensity is outside 99% binomial confidence limits of temperate value.

Definitive tests for macroevolutionary hypotheses can be difficult to frame, but consistency arguments can be designed wherein violation of a logical expectation of a hypothesis constitutes disproof. If incumbency is important in regulating generic diversity latitudinally, then regional diversity dynamics (wherein a taxon's range is not limited by geography) should exhibit reciprocal relationships between extinction rates and invasion or local origination (i.e., local origination preferentially occurs following the removal of incumbent taxa, assuming a reasonably constant climatic regime). One testable prediction is that the low-diversity, high-latitude faunas should exhibit relatively static compositions—a high degree of incumbency—and so should have had about the same generic compositions before the strong Pleistocene glaciations as they do today. Data are not yet available for a complete analysis, but a preliminary test can be made in the Northern Hemisphere Neogene, where bivalve faunas have been described from a few localities north of 60° (Fig. 2). Of 66 genera reported north of 60°N in Pliocene and Pleistocene assemblages, only three

(4.5%) are globally extinct and only five are now locally extinct. Four of the locally extinct genera live today in latitudes at 50°N or above, from where they could easily be introduced into Arctic waters during climatic amelioration (the other locally extinct genus lives to 45°N). In contrast, north temperate bivalves have suffered roughly 12% global extinction plus 8% local extinction, and we estimate the corresponding tropical extinctions to be roughly 8% and 1% respectively.

These numbers must be treated as preliminary. The north temperate fauna is by far the best sampled; the Arctic fauna is less well known, but its spatial homogeneity indicates that fewer samples will capture a large fraction of the biota; the tropical biota is worst sampled, and the numbers recorded here involve rough estimates (see caption of Fig. 2). Note, however, that the use of extinction proportions within a single time frame reduces the sensitivity to sampling of the reported values. For example, for Pliocene–Pleistocene tropical extinction to reach temperate levels would require a twofold error in our estimate of tropical extinction (from ~ 30 to ~ 60) or of tropical diversity (from ~ 450 to ~ 225); the latter is especially unlikely given that Todd et al. (2002) report ~ 200 Pliocene bivalve genera in tropical America alone, omitting the rich faunas of Florida and the Greater Antilles and, more importantly, the great Indo–West Pacific diversity maximum. Thus, the estimates shown here, with a counterintuitive, non-monotonic relation of extinction intensity with latitude and standing diversity, present an interesting challenge to the many hypotheses invoking predominantly direct abiotic controls on the dynamics of the LDG. Even given that our extinction figures are preliminary, there is no evidence that extinction alone can account for or promote the diversity difference between temperate and polar zones.

These new results, though preliminary, are a substantial refinement of the extinction patterns reported by Jablonski et al. (2006). The earlier paper simply compared extinction rates between tropical and extratropical zones, and Arctic diversity is such a small fraction of the extratropical total ($<15\%$) that it had little effect on the first-order signal. Par-

tioning the northern extratropics into temperate and polar zones allows us to show that extinction intensity does not simply increase monotonically with latitude and supports a potential role of biotic factors in the low invasion rates evident for both the Tropics and the poles relative to the temperate zones.

Although temperature may not directly determine standing diversity, its fluctuations may set the pattern of extinction intensities, both being highest in temperate latitudes today and during Pleistocene climate swings (see Jansson 2003). Temperature adaptation is clearly involved in establishing the geographic ranges of many taxa, and as noted above, changes in range end-points accompanying isothermal shifts are well documented from midlatitudes, especially during glacial-interglacial cycles. Our data are insufficient at present to study these relations in detail, but the patterns of midlatitude thermal variability (which coincide with fluctuations in many additional factors) and the patterns of extinction clearly deserve further scrutiny.

Summary and Conclusions

Through much of the Neogene at least, speciation has evidently been easier within low-latitude, high-diversity ecosystems than within high-latitude, low-diversity ecosystems, creating an abundance of young lineages in low latitudes. This dynamic implies that resources are more easily obtained by new species in high-diversity than in low-diversity ecosystems, a counterintuitive observation, particularly in light of apparent resistance of tropical habitats to invasion from high latitudes over both the short and the long term. Such a latitudinal trend in origination could be promoted by ecological feedbacks, such as proposed by advocates of niche construction (e.g., Odling-Smee et al. 2003; Erwin 2007), but the question of why there should be a gradient in feedbacks remains. The rapid diversity rebound in the New World Tropics following a late Neogene extinction pulse (see Todd et al. 2002; O'Dea et al. 2007) might have been partially fueled from higher latitudes, but the huge pool of tropical lineages available as diversification sources would have swamped the much smaller number of potential extratropi-

cal invaders. Combined molecular and paleontological analyses are needed to assess biogeographic sources of the marine Neotropical evolutionary rebound.

Adaptations to the high-latitude environment, whether biotic, physical, or both combined, seem to result in the suppression of per-taxon origination relative to lower latitudes. This would explain the progressive failure of generic lineages to penetrate into increasingly higher latitudes where ecological generalists are most successful and are incumbent. Indeed, such preemptive interactions may be a significant factor in molding the LDG to the gradient of those diversity-dependent environmental conditions that correlate with latitude. The role played by extinction in the dynamics of the LDG would thus be to reduce the incumbent fauna sufficiently below its carrying capacity to provide "openings" for the invasion of new species (Walker and Valentine 1984), some of which would add genera to the region. If a polar extinction spike could be found, our hypothesis might be tested by whether there was a compensatory replacement of lost genera from the temperate biota. At any rate, the lack of any clear difference between temperate and polar extinction rates accords well with the dynamic outlined above. There is no evidence in the data reported here that the extinction rate directly affects carrying capacity or is the primary control on the LDG, although it may push diversity below regional carrying capacity and thus drive temporal or spatial divergence from an idealized trend.

The hypothesis we develop here thus goes counter to classic suggestions that equatorward range limits are set by biotic interactions and poleward limits are set by physical factors (e.g., Dobzhansky 1950; MacArthur 1972). Instead, we suggest that physical environmental factors determine regional differences in the niche breadth of taxa throughout the LDG, with resulting variations in biotic resistance to invasion and local origination. The LDG, and by implication other large-scale spatial variations in diversity, is thus primarily an evolutionary rather than an ecological phenomenon, albeit, as in most evolutionary cases, driven by adaptations to ecological condi-

tions. We suggest that marine latitudinal gradients in diversity-dependent ecological factors produce an OTT dynamic, with a low-latitude source and higher-latitude filters, where the filtering processes are mediated by the incumbency of local populations that belong on average to progressively older and ecologically more generalized lineages at progressively higher latitudes. Moreover, the role of biotic interactions as proximate factors in structuring spatial and temporal diversity patterns will be severely underestimated if, as proposed here, the nature of those interactions varies with physical environmental parameters. Diversity-dependent factors do not only come into play at the high end of the diversity scale. Depending on regional history and environmental context, we suspect that biotas at any diversity level can be at, or distant from, a state in which diversity dependence is a significant force.

Acknowledgments

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Literature Cited

- Allison, P. A., and D. E. G. Briggs. 1993. Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology* 21:65–68.
- Arim, M., S. R. Abades, P. E. Neill, M. Lima, and P. A. Marquet. 2006. Spread dynamics of invasive species. *Proceedings of the National Academy of Sciences USA* 103:374–378.
- Armbrecht, I., I. Pefecto, and J. Vandermeer. 2004. Enigmatic biodiversity correlations: ant diversity responds to diverse resources. *Science* 304:284–286.
- Beard, K. C. 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. *Bulletin of the Carnegie Museum of Natural History* 34:5–39.
- Clark, A., and J. A. Crame. 2003. The importance of historical processes in global patterns of diversity. Pp. 130–151 in T. M. Blackburn and K. J. Gaston, eds. *Macroecology: concepts and consequences*. Blackwell Science, Oxford.
- Connolly, S. R., D. R. Bellwood, and T. P. Hughes. 2003. Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. *Ecology* 84:2178–2190.
- Crame, J. A. 2000. Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of Recent bivalve faunas. *Paleobiology* 26:188–214.
- . 2001. Taxonomic diversity gradients through geological time. *Diversity and Distributions* 7:175–189.
- . 2002. Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas. *Paleobiology* 28:184–207.
- Crame, J. A., and B. R. Rosen. 2002. Cenozoic palaeogeography and the rise of modern biodiversity patterns. *Geological Society of London Special Publication* 177:227–246.
- Crombie, A. D. 1945. On competition between different species of granivorous insects. *Proceedings of the Royal Society of London B* 132:362–395.
- Dobzhansky, Th. 1950. Evolution in the tropics. *American Scientist* 38:209–221.
- Erwin, D. H. 2007. Disparity: morphologic pattern and developmental context. *Palaeontology* 50:57–73.
- Etter, R. J., and J. F. Grassle. 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature* 360:576–578.
- Fine, P. V. A. 2002. The invasibility of tropical forests by exotic plants. *Journal of Tropical Ecology* 18:687–705.
- Footo, M. 2001. Evolutionary rates and the age distributions of living and extinct taxa. Pp. 245–194 in J. B. C. Jackson, S. Lidgard, and F. K. McKinney, eds. *Evolutionary patterns*. University of Chicago Press, Chicago.
- Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88:3–17.
- Gage, J. D., and J. A. Tyler. 1991. *Deep-sea biology*. Cambridge University Press, Cambridge.
- Gaston, K. J., T. M. Blackburn, and J. L. Spicer. 1998. Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution* 13:70–74.
- Gladenkov, Y. B., and V. N. Sinelnikova. 1990. Miocene mollusks and climate in Kamchatka. *Trudy Geologicheskogo Instituta Akademiyi Nauk SSSR* 453:1–173. [In Russian.]
- Goldberg, E. E., K. Roy, R. Lande, and D. Jablonski. 2005. Diversity, endemism and age distribution in macroevolutionary sources and sinks. *American Naturalist* 165:623–633.
- Hewitt, C. L. 2002. Distribution and biodiversity of Australian tropical marine bioinvasions. *Pacific Science* 56:213–222.
- Hickerson, M. J., and C. W. Cunningham. 2006. Nearshore fish (*Pholis gunnellus*) persists across the North Atlantic through multiple glacial episodes. *Molecular Ecology* 15:4095–4107.
- Jablonski, D. 1993. The tropics as a source of evolutionary novelty: the post-Palaeozoic fossil record of marine invertebrates. *Nature* 364:142–144.
- . 2005. Evolutionary innovations in the fossil record: the intersection of ecology, development and macroevolution. *Journal of Experimental Zoology B* 304:504–519.
- Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* 58:21–89.
- Jablonski, D., and J. J. Sepkoski Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–1378.
- Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.
- Jackson, J. B. C., and K. G. Johnson. 2001. Measuring past biodiversity. *Science* 293:2401–2404.
- Jakobsson, M., J. Backman, B. Rudels, J. Mycander, M. Frank, L. Mayer, W. Jokat, F. Sangiorgi, M. O'Regan, H. Brinkhuis, J. King, and K. Moran. 2007. The early Miocene onset of a ventilated circulation regime in the Arctic Ocean. *Nature* 447:986–990.
- Jansson, R. W. 2003. Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society of London B* 270:583–590.
- Jones K. E., W. Sechrest, and J. L. Gittleman. 2005. Age and area revisited: identifying global patterns and implications for conservation. Pp. 141–165 in A. Purvis, J. L. Gittleman, and T.

- Brooks, eds. *Phylogeny and conservation*. Cambridge University Press, Cambridge.
- Kendrick, G. W., K. H. Wyrwoll, and B. J. Szabo. 1991. Pliocene-Pleistocene events and history along the western margin of Australia. *Quaternary Science Reviews* 10:419–439.
- Kitamura, A., H. Omote, and M. Oda. 2000. Molluscan response to early Pleistocene rapid warming in the Sea of Japan. *Geology* 28:723–726.
- Knudsen, J. 1979. Deep-sea bivalves. Pp. 195–224 in S. van der Spoel, A. C. van Bruggen, and J. Lever, eds. *Pathways in malacology*. Bohn, Scheltema and Holkema, Utrecht.
- Kreft, H., and W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA* 104:5925–5930.
- Krug, A., D. Jablonski, K. Roy, and J. W. Valentine. 2006. Contrasting bivalve latitudinal diversity gradients shaped by Cenozoic origination patterns. *Geological Society of America Abstracts with Programs* 38(7):169.
- Krug, A. Z., D. Jablonski, and J. W. Valentine. 2008. Species-genus ratios reflect a global history of diversification and range expansion in marine bivalves. *Proceedings of the Royal Society of London B* (published online 13 February 2008).
- Laptikhovskiy, V. 2006. Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology* 27:7–14.
- Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. *Biogeography*, 3d ed. Sinauer, Sunderland, Mass.
- Longhurst, A. 1998. *Ecological geography of the sea*. Academic Press, San Diego.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper and Row, New York.
- Martin, P. R., F. Bonier, and J. J. Tewksbury. 2007. Revisiting Jablonski (1993): cladogenesis and range expansion explain latitudinal variation in taxonomic richness. *Journal of Evolutionary Biology* 20:930–936.
- Miller, A. I. 1997. A new look at age and area: the geographic and environmental expansion of genera during the Ordovician Radiation. *Paleobiology* 23:410–419.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A. McPeck, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel, and M. Turelli. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10:315–331.
- O'Dea, A., J. B. C. Jackson, H. Fortunato, J. T. Smith, L. D'Croz, K. G. Johnson, and J. A. Todd. 2007. Environmental change preceded Caribbean extinction by 2 million years. *Proceedings of the National Academy of Sciences USA* 104:5501–5506.
- Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003. *Niche construction: the neglected process in evolution*. Princeton University Press, Princeton, N.J.
- Ogasawara, K. 1994. Neogene paleogeography and marine climate of the Japanese Islands based on shallow-marine molluscs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108:335–351.
- Paulay, G., L. Kirkendale, G. Lambert, and C. Meyer. 2002. Anthropogenic biotic interchange in a coral reef ecosystem: a case study from Guam. *Pacific Science* 56:403–422.
- Raffi, S., S. M. Stanley, and R. Marasti. 1985. Biogeographic patterns and Plio-Pleistocene extinction of *Bivalvia* in the Mediterranean and southern North Sea. *Paleobiology* 11:368–388.
- Rejmánek, M. 1996. Species richness and resistance to invasions. Pp. 153–172 in G. Orians, R. Dirzo, and J. H. Cushman, eds. *Diversity and processes in tropical forest ecosystems*. Springer, Berlin.
- Rex, M. A., J. A. Crame, C. T. Stuart, and A. Clarke. 2005. Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity? *Ecology* 86:2288–2297.
- Ribas, C. R., and J. H. Schoeder. 2006. Is the Rapoport effect widespread? Null models revisited. *Global Ecology and Biogeography* 15:614–624.
- Roberts, C. M., C. J. McClean, J. E. N. Veron, J. P. Hawkins, G. R. Allen, D. E. McAllister, C. G. Mittermeier, F. W. Schueler, M. Spalding, F. Wells, C. Vynne, and T. B. Werner. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295:1280–1284.
- Rosenzweig, M. L. 1995. *Species diversity in time and space*. Cambridge University Press, Cambridge.
- Rosenzweig, M. L., and R. D. McCord. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology* 17:202–213.
- Roy, K., and E. E. Goldberg. 2007. Origination, extinction and dispersal: integrative models for understanding present-day diversity gradients. *American Naturalist* 170(Suppl.):S71–S85.
- Roy, K., D. Jablonski, and J. W. Valentine. 1994. Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for "Rapoport's rule." *Proceedings of the National Academy of Sciences USA* 91:8871–8874.
- . 1995. Thermally anomalous assemblages revisited: patterns in the extraprovincial latitudinal range shifts of Pleistocene marine mollusks. *Geology* 23:1071–1074.
- . 2000. Higher taxa in biodiversity studies: patterns from eastern Pacific marine mollusks. *Philosophical Transactions of the Royal Society of London B* 351:1605–1613.
- Roy, K., D. Jablonski, J. W. Valentine, and G. Rosenberg. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences USA* 95:3699–3702.
- Ruggiero, A., and V. Werenkraut. 2007. One-dimensional analyses of Rapoport's Rule reviewed through meta-analysis. *Global Ecology and Biogeography* 16:401–414.
- Sax, D. F. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography* 28:139–150.
- Sax, D. F., and S. D. Gaines. 2006. The biogeography of naturalized species and the species-area relationship: reciprocal insights to biogeography and invasion biology. Pp. 449–480 in M. W. Cadotte, S. M. McMahon, and T. Fukami, eds. *Conceptual ecology and invasions biology: reciprocal approaches to nature*. Kluwer, Dordrecht, The Netherlands.
- Sax, D. F., J. J. Stachowicz, J. H. Brown, J. F. Bruno, M. N. Dawson, S. D. Gaines, R. K. Grosberg, A. Hastings, R. D. Holt, M. M. Mayfield, M. I. O'Connor, and W. R. Rice. 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution* 22:465–471.
- Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford University Press, Oxford.
- Smith, H. S. 1935. The role of biotic factors in the determination of population densities. *Journal of Economic Entomology* 28: 873–898.
- Stachowicz, J. J., and D. Tilman. 2005. Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. Pp. 41–64 in D. F. Sax, J. S. Stachowicz, and S. D. Gaines, eds. *Species invasion: insights into ecology, evolution and biogeography*. Sinauer, Sunderland, Mass.
- Stevens, G. C. 1989. The latitudinal gradient in geographic range: how so many species co-exist in the tropics. *American Naturalist* 133:240–256.
- Tankard, A. J. 1975. Thermally anomalous Late Pleistocene molluscs from the south-western Cape Province, South Africa. *Annals of the South African Museum* 69:17–45.
- Taylor, J. D., and C. N. Taylor. 1977. Latitudinal distribution of

- predatory gastropods on the Eastern Atlantic shelf. *Journal of Biogeography* 4:73–81.
- Thorsen, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* 25:1–45.
- Todd, J. A., J. B. C. Jackson, K. G. Johnson, H. M. Fortunato, A. Heitz, F. Alvarez, A. Marcos, and P. Jung. 2002. The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society of London B* 269:571–578.
- Valentine, J. W. 1961. Paleogeologic molluscan geography of the Californian Pleistocene. University of California Publications in Geological Science 34:309–442.
- . 1972. Conceptual models of ecosystem evolution. Pp. 192–215 in T. J. M. Schopf, ed. *Models in paleobiology*. Freeman, Cooper, San Francisco.
- . 1973. Evolutionary paleoecology of the marine biosphere. Prentice-Hall, Englewood Cliffs, N.J.
- . 1983. Seasonality: effects in marine benthic communities. Pp. 121–156 in M. J. S. Tevesz and P. L. McCall, eds. *Biotic interactions in recent and fossil benthic communities*. Plenum, New York.
- Valentine, J. W., and F. J. Ayala. 1978. Adaptive strategies in the sea. Pp. 323–345 in B. Battaglia and J. A. Beardmore, eds. *Marine organisms: genetics, ecology, and evolution*. Plenum, New York.
- Valentine, J. W., K. Roy, and D. Jablonski, 2002. Carnivore/non-carnivore ratios in northeastern Pacific marine gastropods. *Marine Ecology Progress Series* 228:153–163.
- Valentine, J. W., D. Jablonski, S. M. Kidwell, and K. Roy. 2006. Assessing the fidelity of the fossil record by using marine bivalves. *Proceedings of the National Academy of Sciences USA* 103:6599–6604.
- Vermeij, G. J. 1978. *Biogeography and adaptation*. Harvard University Press, Cambridge.
- . 1991. When biotas meet: understanding biotic interchange. *Science* 253:1099–1104.
- . 2005a. From phenomenology to first principles: toward a theory of diversity. *Proceedings of the California Academy of Sciences*, series 4, 56(Suppl. I, No. 2):12–23.
- . 2005b. Invasion as expectation: a historical fact of life. Pp. 315–339 in D. F. Sax, J. S. Stachowicz, and S. D. Gaines, eds. *Species invasion: insights into ecology, evolution and biogeography*. Sinauer, Sunderland, Mass.
- Walker, T. D., and J. W. Valentine, 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *American Naturalist* 124:887–899.
- Ward, L. W. 1992. Molluscan biostratigraphy of the Miocene Middle Atlantic coastal plain of North America. *Virginia Museum of Natural History Memoir* No. 2.
- Webb, T. J., and K. J. Gaston. 2000. Geographic range size and evolutionary age in birds. *Proceedings of the Royal Society of London B* 267:1843–1850.
- Wiens, J. J., M. C. Brandley, and T. W. Reeder. 2006. Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. *Evolution* 60:13–141.
- Wier, J. T., and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315:1574–1576.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273–309.
- Willis, J. C. 1922. *Age and area: a study in geographical distribution and origin of species*. Cambridge University Press, Cambridge.