Synthesis

Shaping the Latitudinal Diversity Gradient: New Perspectives from a Synthesis of Paleobiology and Biogeography

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abstract: An impediment to understanding the origin and dynamics of the latitudinal diversity gradient (LDG)—the most pervasive large-scale biotic pattern on Earth—has been the tendency to focus narrowly on a single causal factor when a more synthetic, integrative approach is needed. Using marine bivalves as a model system and drawing on other systems where possible, we review paleobiologic and biogeographic support for two supposedly opposing views, that the LDG is shaped primarily by (*a*) local environmental factors that determine the number of species and higher taxa at a given latitude (in situ hypotheses) or (*b*) the entry of lineages arising elsewhere into a focal region (spatial dynamics hypotheses). Support for in situ hypotheses includes the fit of present-day diversity trends in many clades to such environmental factors as temperature and the correlation of extinction intensities in Pliocene bivalve faunas with net regional temperature changes. Support for spatial dynamics hypotheses includes the age-frequency distribution of bivalve genera across latitudes, which is consistent with an out-of-the-tropics dynamic, as are the higher species diversities in temperate southeastern Australia and southeastern Japan than in the tropical Caribbean. Thus, both in situ and spatial dynamics processes must shape the bivalve LDG and are likely to operate in other groups as well. The relative strengths of the two processes may differ among groups showing similar LDGs, but dissecting their effects will require improved methods of integrating fossil data with molecular phylogenies. We highlight several potential research directions and argue that many of the most dramatic biotic patterns, past and present, are likely to have been generated by diverse, mutually reinforcing drivers.

Keywords: extinction, speciation, geographic range dynamics, phylogeny, historical biogeography, paleobiology.

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Introduction

The latitudinal diversity gradient (LDG), the most pervasive large-scale biological pattern on Earth, has been documented and debated for more than two centuries. Multiple reviews have attested to the increase in diversity of species and higher taxa from poles to tropics and cataloged the many hypotheses on underlying mechanisms (e.g., Pianka 1966; Rohde 1992; Gaston 2000; Hillebrand 2004; Mittelbach et al. 2007; Krug et al. 2009*b*; Donoghue and Edwards 2014; Fine 2015; Schluter 2016), leading Brown (2014, p. 9) to state that "even as the patterns have become clearer . . . the explanations have remained elusive and controversial." However, others have suggested that the many proposed explanations are beginning to coalesce (e.g., Fine 2015). In this essay, we go one step further to argue that a number of supposedly opposing hypotheses about the LDG actually represent different facets that should be integrated to gain a fuller understanding of the origin and maintenance of this biodiversity pattern.

One such artificial dichotomy, the chief focus of this essay, involves hypotheses that the equator-to-pole profile of the LDG is essentially shaped by local environmental factors that determine the number of species and higher taxa at a given latitude (for brevity, we will call these in situ hypotheses), as opposed to hypotheses that center on the long-term spatial dynamics of clades across latitudes. The crux of this dichotomy is the explanatory power of past and present conditions within the region where diversity is being measured, as opposed to processes that closely link diversity in the focal region to events outside it. We argue that, in fact, in situ processes and spatial dynamics have likely shaped the modern LDG in concert, as illustrated by the simple conceptual model in figure 1. Consider two adjacent regions, α and β, which can represent two adjacent latitudinal bands or biogeographic provinces anywhere along the LDG. (Note that the focus of this essay is on the mechanisms underlying the shape of the full LDG rather than

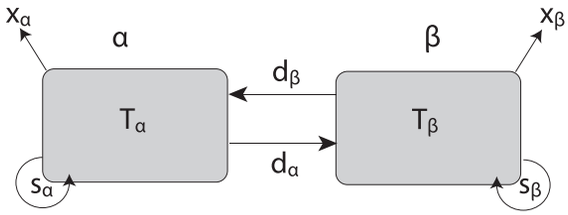

Figure 1: Simple model for diversity dynamics. The taxonomic diversity in regions α and β are functions of in situ factors—environmental and habitat characteristics (T_α and T_β), within-region rates of speciation (s_α and s_β), and extinction rates (x_α and x_β)—and dispersal into each area (d_α and d_β), that is, the larger-scale spatial dynamic (for further details, see Goldberg et al. 2005; Jablonski et al. 2006; Roy and Goldberg 2007).

those responsible for a binary, tropical-vs.-extratropical contrast in richness; the latter would mostly fall under an in situ heading, aside from those hypotheses holding that tropical diversity is promoted by the influx of taxa from higher latitudes.) The richness of each region at a given time is partly a function of (i) the environmental and habitat characteristics of each region (T_α and T_β), (ii) the speciation rates in each region (s_α and s_β), and (iii) their respective extinction rates (x_α and x_β), which together constitute the in situ component because they operate within each region. In addition, the richness of each region is also a function of dispersal into each area (d_α and d_β), a spatial dynamic that involves regional processes elsewhere that affect the focal area. Clearly, all of these processes should be evaluated together for a comprehensive understanding of the LDG. Yet, as discussed below, traditionally they have been treated separately, and relatively little is known about how they interact.

We will support this integrative view by a combination of present-day and fossil data that provide evidence for each type of dynamic and, therefore, for their simultaneous operation. We frame our discussion using the marine Bivalvia, which have become a model system for large-scale spatial and temporal analyses for at least three reasons. First, their well-documented biogeography shows a strong LDG (fig. 2) that mirrors that of other groups on land and sea (Hillebrand 2004; Tomasovych et al. 2016). Second, they exhibit relatively high taxonomic, phenotypic, and functional diversity, including a wide range of trophic groups ranging from suspension feeding through chemo- and photosymbiosis to predation and parasitism. And third, their rich fossil record allows robust estimates of origination, regional and global extinction, and geographic range dynamics through time (Crame 2000*a*, 2000*b*, 2002; Jablonski et al. 2006, 2013; Bieler et al. 2013; Berke et al. 2014; Huang et al. 2015; Mondal and Harries 2016). The ideas presented here should apply broadly across different groups of organisms, and where possible we draw on examples from other groups as well. We will also briefly touch on a related (false) dichotomy, that is, whether the tropics are a cradle or museum of biodiversity.

Evidence for In Situ Controls

Many analyses, both marine and terrestrial, have found that present-day temperature (annual mean and, to some extent, variance) along with a handful of other physical factors, such as precipitation on land and productivity in the sea, are powerful first-order predictors of the profile of the LDG on global and continental scales (Fine 2015 and references therein) and of the boundaries between biogeographic units, such as provinces (Olson et al. 2001; Lomolino et al. 2010; Belanger et al. 2012; Briggs and Bowen 2012). The consensus, reasonably, has been that such correlations provide strong evidence for in situ controls and that species and higher-taxon richness within latitudinal bands or provinces track climate almost instantaneously, in that diversity often fits well with present-day factors despite the enormous changes in climate at most locations over the past 18,000 years. However, the species-rich bathyal (deep-sea) benthos suggests that tropical temperatures are not necessary to generate and maintain high levels of diversity (Rex and Etter 2010; Valentine and Jablonski 2015). One hypothesis is that high bathyal diversity indicates a role for damped seasonality in, among other potential factors, temperature and organic carbon flux (and thus trophic stability), in contrast to the cold but more

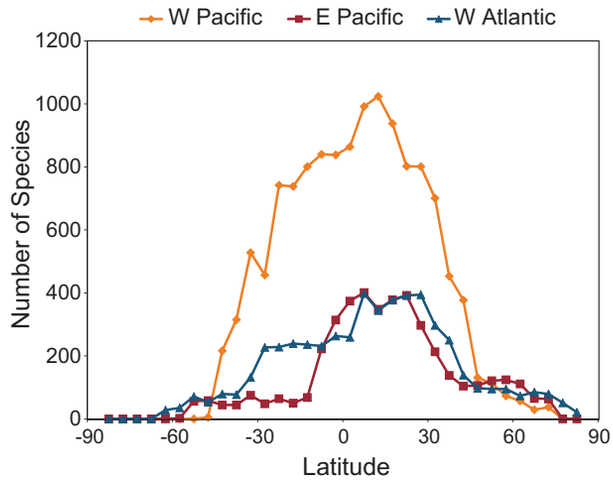

Figure 2: Bivalve latitudinal diversity gradients (species and genus level) at shelf depths (0–200 m) along three well-sampled coastlines. Compiled from the primary literature and museum collections (data from Tomasovych et al. 2016).

seasonal and depauperate polar sea (Valentine and Jablonski 2015). More generally, while a strong correlation between latitudinal trends in mean annual temperature and regional species richness is frequently emphasized (including for bivalves; Roy et al. 1998), many other environmental variables covary along this gradient, as do such historical effects as changes in past climate and habitats (e.g., those driven by Pleistocene glaciations). This multitude of potential drivers makes it difficult to evaluate the role played by different present-day variables and to separate present-day and historical factors (e.g., Jetz et al. 2004; Ricklefs 2004; Erwin 2009; Field et al. 2009; Svenning et al. 2015; Valentine and Jablonski 2015).

Large-scale natural experiments can shed light on the role played by in situ climate changes in shaping the LDG, and inferences about the variability of past climatic and other environmental conditions have been used to explain regional diversity patterns. The bivalve fossil record shows that regional extinction is strongly correlated with net temperature change since the mid-Pliocene and regional extinction in Pliocene bivalve faunas (fig. 3). In particular, the striking correspondence between modest net temperature changes and regional losses in the warm-temperate Pliocene faunas is consistent with the view that such historical factors as past climatic changes and extinctions have played a major role in shaping the modern LDG (e.g., Mannion et al. 2014). The temperature differences between modern and full-glacial Pleistocene conditions were greater than those in the Pliocene, albeit with roughly parallel interregional patterns (see Annan and Hargreaves 2013; Precht and Aronson 2016), and so could have contributed to, or reinforced, the observed trend. In any case, bivalves show differential regional extinctions with latitude that are positively related to net regional cooling over the past 3 million years and, probably, to the distribution of temperature minima in the Pleistocene. Most of these extinctions were regional, with individual clades contracting equatorward in the face of climate cooling (Valentine et al. 2013), progressively sharpening the LDG as the poles shifted to a refrigerated state (albeit with smaller, repeated distributional shifts during glacial/interglacial cycles). Detailed interregional analyses comparing the effects of time-integrated temperature change or maximum regional excursions against net biotic change would be valuable.

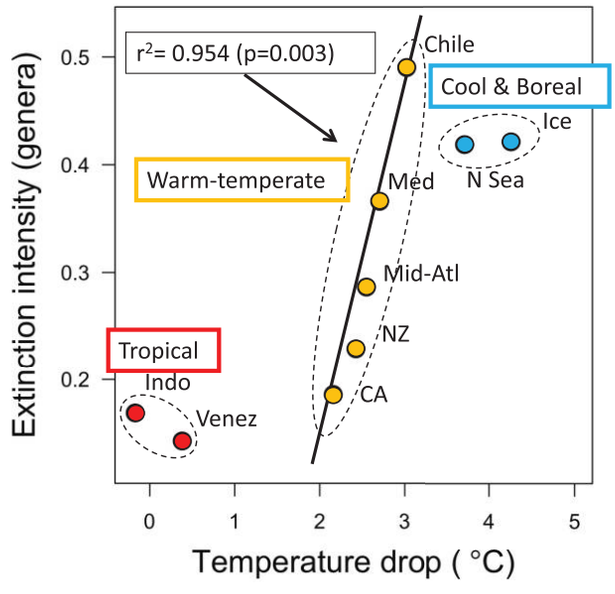

Figure 3: Regional extinction in Pliocene faunas versus net temperature change from the Pliocene to the present day. Regional temperature changes are estimated using a spatially explicit model of Pliocene paleotemperatures based on stable isotopes in microfossils (Dowsett et al. 2010, 2013) and thus are independent of molluscan distributional data; bivalve data are from Valentine et al. (2013) and Jablonski et al. (2013). CA = California; Indo = Indonesia; Ice = Iceland; Med = Mediterranean; Mid-Atl = Mid-Atlantic states, United States; N Sea = North Sea region; NZ = New Zealand; Venez = Venezuela.

The pattern in figure 3 also supports the more specific view that regions that experienced lesser climate change have harbored, and perhaps have generated, more diversity than regions that experienced greater changes (e.g., Jansson and Dynesius 2002; Pyron and Wiens 2013; Mannion et al. 2014; Fine 2015; Claramunt and Cracraft 2015; Pulido-Santacruz and Weir 2016). The effects of such variation can be manifest at a variety of scales and locations. For example, within the tropics, present-day local diversity in marine fishes is inversely related to distance from historically stable reef areas (Pellissier et al. 2014). In the temperate zones, the high plant diversity in the South African Cape Floristic Region has been attributed to the apparently damped climate fluctuations for its latitude (Dynesius and Jansson 2000; Schnitzler et al. 2011; for additional examples, see also Jansson 2003; Svenning et al. 2015), and climate velocity—defined as the rate of displacement of climatic conditions across a region—has been shown to influence geographic patterns of endemism in multiple vertebrate groups (Sandel et al. 2011), which in turn affects their LDGs. In the deep-sea benthos, more direct analyses using estimates of paleotemperature and paleoproductivity show that regional species richness of deep-sea invertebrates responded predictably to past changes in climate (Hunt et al. 2005; Yasuhara et al. 2012).

Taken together, figure 3, the extensive literature showing a close relation today between both marine and terrestrial diversity and regional climate, and the smaller literature relating fossil diversity to climate shifts (Erwin 2009; Mannion et al. 2014) strongly suggest that regional diversity can change substantially when the environmental pa-

rameters shift strongly. For bivalves, such climate-driven steepening of the LDG does not appear to be phylogenetically patterned, at least not at the family level, where comprehensive phylogenetic data are available (Bieler et al. 2014). Comparing diversity changes along each of the temperate coasts of North America from the Pliocene to the present day, a given family may show different extinction rates and/or dispersal dynamics on different coasts (Huang et al. 2015). A better predictor of clade behavior in the face of cooling climates is the geographic range size of species at the Pliocene starting point, with the narrowest-ranging species most prone to disappear from the focal region (Huang et al. 2015; see also Saupe et al. [2015], who found that a measure of niche breadth lacks the predictive power shown by geographic range per se). This result is not surprising in that those species most able to tolerate and disperse among a range of latitudes and environments might be expected to survive longest, but it usefully demonstrates that this tolerance effect can override family-level clade membership. Studies of present-day terrestrial birds and mammals, using more indirect methods, have also concluded that climate changes "can force multiple groups into similar diversity patterns even when evolutionary trajectories differ" (Hawkins et al. 2012, p. 825). These findings drive home the message that a given clade can attain similar diversities in two regions in the absence of similar diversification dynamics and that different diversities for a given clade in two regions today need not signal a long divergent history.

Evidence for Spatial Dynamics

Changing climates, and thus tracking of in situ environmental change with or without lags, are not the only impetus for large-scale biogeographic shifts. Our initial work, and that of many others, on the dynamics underlying the LDG was motivated by Stebbins's (1974) famous question: are the tropics a cradle or a museum of diversity? Stebbins used the cradle metaphor for regions that are diversity generators, presumably with high origination rates, while museums are areas that accumulate diversity, presumably with low extinction rates. Although such a binary characterization of the evolutionary drivers of the LDG has led to considerable empirical work, this dichotomy is increasingly proving to be a false one. The fossil record shows that, over the past 12 million years, bivalve genera preferentially originated in the tropics and expanded their ranges poleward over time—even in the Pleistocene, during times of glaciated poles and steep thermal gradients—while maintaining their tropical presence (Jablonski et al. 2006, 2013 [the latter with substantially improved data based on further integration of literature and museum records]). The pattern is particularly striking given that the sampling is strongly biased to the temperate zones (Valentine et al. 2013), so that some of the clades that originated in the tropics would not have entered into the fossil record until they entered the midlatitudes, thereby underestimating the strength of the dynamic.

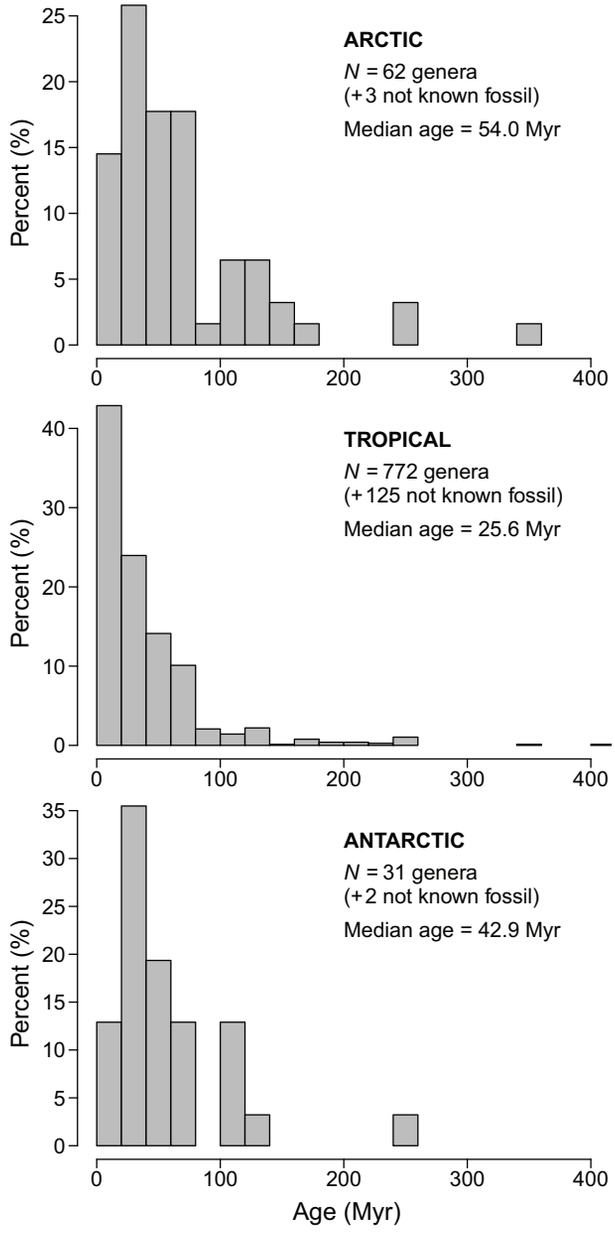

Figure 4: Geologic ages of bivalve genera at high and low latitudes, showing a deficiency of young taxa near both poles and a long tail of older taxa in all three regions. Frequency distributions for the Arctic and Antarctic differ significantly from that of the tropics (Komogorov-Smirnov test; tropics vs. Arctic, $P < .001$; tropics vs. Antarctic, $P = .004$) but not from each other ($P = .78$). Genus ages are given in table S1 in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.qd53c (Jablonski et al. 2017).

Because nearly all bivalve clades that expand out of the tropics (OTT) maintain their presence in the tropics even as they push poleward and because the highest latitudes evidently have low origination rates, the polar regions harbor very few young genera while the tropics have many, with a median age roughly half that of the polar fauna (e.g., Goldberg et al. 2005). However, tropical genera also have a long tail to their age distribution, which includes ~90% of the taxa that constitute the polar tails (fig. 4). Thus, the tropics are both a cradle and a museum of diversity in that they harbor both the oldest and the youngest genera. The poles are mainly a museum of diversity, as they harbor mostly older genera. Of course, present-day age distributions in a given region are uninformative about when taxa actually arrived, but the fossil data can determine the polarity of such movement.

These latitudinal dynamics could still fit into an in situ paradigm if the OTT genera were simply filling gaps left by regional extinctions to keep the regional biota in equilibrium with key environmental variables. Tests on, for example, ecological equivalency between extinctions and successful OTT range expansions would therefore be valuable. However, comparison of West Pacific and West Atlantic diversity patterns falsify any simple in situ hypothesis. Southeastern Japan and southeastern Australia, each firmly lodged today in the temperate zone, contain 30% and 14% more species, respectively, than the Caribbean (table 1; see also Tittensor et al. 2010, in which diversity maps incorporating a variety of marine groups show similar or greater coastal diversity in one or both of our two temperate regions relative to the tropical Caribbean, aside from two strongly tropical clades [corals and mangroves]). In situ models would predict the opposite: the Caribbean has an order of magnitude more shelf area than either of the temperate provinces; its mean annual sea surface temperature is 5°–6°C warmer and significantly less seasonal; it is topologically and ecologically more complex, with coral reefs and a scatter of islands of various sizes in contrast to the essentially linear temperate provinces; and it almost certainly hosts a greater variety and intensity of biotic interactions, another factor posited to promote taxonomic diversity (e.g., Mittelbach et al. 2007; Schemske et al. 2009). Diversity is evidently spilling over from the massively diverse west Pacific tropical region into the two adjacent temperate provinces, to an extent that overwhelms the simple environment-diversity relationships that are often seen when examining a single coastline or cumulative diversity in global latitudinal bands.

The very low diversity near the poles relative to diversity maxima in all tropical regions also has analytical consequences: a global model focusing exclusively on the equator-pole gradient will tend to downplay longitudinal interocean differences, which, though little studied, have the potential to be highly informative about the interaction of processes that set large-scale diversity patterns. For example, linear models linking diversity to in situ environmental factors will tend to derive strong support from extreme polar and tropical values, which then drive the conclusions. Yet the deviations from model predictions at midlatitudes and elsewhere, often dismissed as noise, actually represent biologically informative variance. To be sure, some interocean differences arise from historical events, the consequences of which are chiefly restricted to a single ocean basin. The uplift of the Panamanian Isthmus and the oceanographic response was such an event, potentially accounting in part for the surprisingly low modern Caribbean diversity. Although spatially heterogeneous within the Caribbean, this turnover event involved a 14% extinction of bivalve genera and subgenera, by one estimate, but is followed by a 20% diversity rebound on a per-taxon basis (Todd et al. 2002) and so is unlikely to account by itself for the observed discordance between environment and diversity seen in these tropical-temperate contrasts.

Table 1: Comparisons of bivalve faunas of the Caribbean, southeastern Australia, and southeastern Japan

Region	No. species	Shelf area (km^2)	Latitudinal extent (°)	Mean annual sea-surface temperature (°)
SE Japan	769	71,200	7	21.4
Caribbean	537	912,100	27	27.0
SE Australia	612	61,750	14	22.3

Note: The Caribbean Province is taken to extend from southern Florida and the Yucatan Peninsula to the mouth of the Amazon, the southeastern Japan Province is taken to extend from the southern tip of Kyushu to the Boso Peninsula, and the southeastern Australian (Peronian) Province is taken to encompass southern Queensland and New South Wales (for coastal marine biogeographic compartments, see Spalding et al. 2007; Belanger et al. 2012; Briggs and Bowen 2012). Caribbean data are available in datafile S1 of Jablonski et al. (2013). Northeastern Australia and southeastern Japan species lists are provided in table S2 in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.qd53c (Jablonski et al. 2017). Shelf area and latitudinal extent were estimated using ArcGIS. Mean annual sea-surface temperature was calculated from MODIS (http://modis.gsfc.nasa.gov/).

Synthesis and Future Directions

Large-scale diversity patterns are set by the spatial and temporal dynamics of origination, extinction, and geographic range shifts. These dynamics must operate within an environmental framework so that constraints on diversity imposed by the physical and biotic environment are also important. The role played by environmental controls has been corroborated in both paleontological and neontological data sets via the fit of regional diversity variations—

and thus the slope of LDGs—to regional variation in environmental factors, although a key question, whether regional diversities are truly "saturated," remains a subject of debate (Ricklefs 2007; Wiens 2011; Harmon and Harrison 2015; Rabosky and Hurlbert 2015; Svenning et al. 2015; Marshall and Quental 2016). The responsiveness of regional diversities to past warming and cooling episodes, the rebounds associated with global extinction events (Krug et al. 2009*a*; Foote 2010), and the apparent positive relation between perturbations in recipient regions and the subsequent entry of range-expanding taxa (Vermeij 2005*a*, with 2005*b* a counterexample; Valentine et al. 2008; Pires et al. 2015), give indirect support for some form of diversity dependence for these dynamics, although distinguishing between limits set by physical factors and strictly biotic ones is difficult and little explored at this scale. The fact that postextinction rebounds often achieve higher richness levels and can reset diversification rates (e.g., Foote 2010; Krug and Jablonski 2012) and that introduced species can often produce increases in regional diversity (Rosenzweig 2001; Sax and Gaines 2008; and many others) suggest a form of loose diversity dependence that does not require saturation in the strict sense (i.e., with origination or immigration close to zero absent extinction). Approaches that go beyond taxonomic counts or rates would be valuable. For example, authors have yet to demonstrate straightforward replacements among taxa in adaptive zones or functional categories, as might be expected if diversity saturation was the rule. More complex turnovers are imaginable—for example, involving changing levels of specialization with changing climates and thus a lack of straightforward replacements—but will be correspondingly more difficult to identify. In any case, more dynamic steady states that relate to a shifting ceiling but are held well below it by extinction (so that origination is damped but not halted) seem more consistent with large-scale, long-term observations (e.g., Walker and Valentine 1984; Miller and Sepkoski 1988; Jablonski 2008; Foote 2010; Cornell 2013; Marshall and Quental 2016).

An unresolved issue related to diversity saturation that is specific to the LDG involves differences among higher taxa in the ability of their temperate-zone lineages to enter the tropics. The imbalance is great in bivalves and plants, where expansion OTT greatly exceeds examples of reverse flow, in contrast to the apparently unimpeded ability of the tropics to host continued origination in situ. The imbalance is weaker in amphibians and birds, although their tropical entries often occur, or at least are initiated, at high elevations, suggesting that lineages are tracking climates even as they shift latitudes, so that the proper comparison is the fraction of such taxa that then expand into lowland habitats (see Pyron and Wiens 2013; Kennedy et al. 2014).

The intuitively appealing link between the steepening of the latitudinal thermal gradient and the steepening of the LDG, as in our bivalve analyses, is supported by other lines of post-Paleozoic fossil evidence on land and sea, which show shallow LDGs during warm intervals and steepening ones with cooling (Crame 2002; Rose et al. 2011; Fenton et al. 2016; Marcot et al. 2016). However, Powell (2007) has argued that a major late Paleozoic phase of global cooling preferentially removed tropical endemic brachiopods and therefore weakened the LDG, in contrast to most inferences for Cenozoic cooling, which as cited above evidently diminished extratropical diversity but left tropical diversity unscathed or enhanced and thereby strengthened the LDG (fig. 3). Yet to be determined is whether, for example, late Paleozoic glacial episodes differed fundamentally from late Cenozoic ones, late Paleozoic brachiopods differed fundamentally from post-Paleozoic bivalves and other groups found to have steepened their LDGs with glaciations, or late Paleozoic biotas present taxonomic or sampling issues that undermine the comparability of the patterns.

The biogeographic dynamics in greenhouse worlds, such as the early Cenozoic, have been studied less than the biotic responses to refrigerating poles, as the latter led to the present-day configuration. This gap should be remedied, as the response of the LDG to global warming in the geologic past or the anthropogenically warmed future is of much theoretical and practical interest. Assuming that shallowing LDGs under global warming is the norm, as the bulk of the available evidence indicates, the in situ hypothesis would have the shallowing occur by local origination at higher latitudes, whereas spatial dynamics would drive shallowing by range expansion from lower latitudes. Both mechanisms evidently operated during the mid-Pliocene warm interval (Huang et al. 2015), but more rigorous phylogenetic and biogeographic analyses of the Pliocene biota and analyses of other warming intervals are needed to determine the relative importance of these processes on land and sea and among clades.

Even with today's steep thermal gradients, some clades lack a strong LDG globally, and some even show an inverse gradient, with diversity minima in the tropics. Such contrarian trends are known in a few terrestrial, marine benthic, and marine pelagic groups, usually embedded within larger clades showing more conventional LDGs (Roy et al. 2000; Krug et al. 2007; Kindlmann et al. 2007; Lucifora et al. 2011; but see Quicke 2012 and Lees et al. 2014 on sampling issues in ichneumonid wasps and gracilariid moths, respectively). Contrarians are neglected vehicles for testing hypotheses on factors promoting "normal" LDGs. For example, contrarian marine bivalve families tend to exhibit life-history strategies involving relatively low fecundities, high per-offspring maternal investment, and low dispersal abilities, which appear to be increasingly advantageous with increasing latitude, likely owing to slowing of development

at low temperatures and high seasonality (Roy et al. 2000; Krug et al. 2007). Diversity maxima for these bivalve clades tend to be centered around the younger genera, implying higher origination rates in midlatitudes for the contrarian groups (Krug et al. 2007; but also see Pyron and Burbrink [2009], who argue for early colonization of the temperate zone and strong niche conservatism in a contrarian snake tribe).

Life histories may contribute to patterns within major marine groups, but we do not know how differences in dispersal relate to marine-terrestrial comparisons. Most terrestrial groups arguably have lower dispersal abilities than marine mollusks bearing pelagic larvae, but mammals, herps, insects, and plants demonstrably tracked high-frequency, large-amplitude Pleistocene climate changes across hundreds of kilometers (Elias 1984; Holman 1995, 1998; Jackson and Blois 2015; Maguire et al. 2015) and thus are quite capable of moving rapidly over wide distances on the relevant timescales. The critical issue does not appear to be dispersal ability per se—even wide-ranging mollusks tend to track isotherms rather than cross them (Jablonski et al. 2013)—but the ability to establish viable populations in novel climate zones. This ability may still hinge on life history (e.g., per capita fecundity of colonists, as in Roy et al. 2001, 2002), but serious comparative analyses from this perspective have not begun.

Present-day distributions are powerful vehicles for evaluating links between diversity and in situ factors, and the integration of phylogenetic models and modern biogeographic data has the potential of becoming increasingly robust, particularly as paleontological data are brought into the mix. Spatial and temporal dynamics are difficult to derive with confidence from information on extant diversity alone. For example, high extinction rates in temperate zones and unexceptional origination rates in the tropics have been inferred for squamates (Pyron 2014) and birds (Pulido-Santacruz and Weir 2016), and carnivorans are inferred to have temperate extinction and dispersal *into* the tropics (Rolland et al. 2015), using phylogenies that include extant tips. However, some results are based on model comparisons using GeoSSE and related methods, which can be unreliable under certain circumstances (Maddison and FitzJohn 2015; Rabosky and Goldberg 2015). More importantly, analyses relying on extant taxa may not produce reliable estimates of past extinction or spatial shifts (Quental and Marshall 2010; Rabosky 2010), especially given an overarching assumption of a stochastically constant extinction rate. As discussed above, the regional extinctions in the Plio-Pleistocene provide one example of the violation of this assumption, especially since many areas have not seen later evolutionary recoveries. The spatial dynamics described above also indicate that the age of a lineage, whether inferred paleontologically or by estimates from molecular phylogenies, is a poor estimator of the arrival time of that lineage in a region.

Despite our advocacy of integrated studies, we are not arguing that paleontological data can be applied to macroevolutionary and macroecological investigations any less critically than other types of data. Paleontological data can provide a direct window to the spatial and diversification dynamics underpinning modern biodiversity, but spatially structured sampling biases in fossil preservation, discovery, and sampling as well as in publication can generate artificial signal and not simply noise (e.g., Valentine et al. 2013; Hannisdal et al. 2016). For example, the apparent inverse LDGs in Mesozoic dinosaurs, with diversity maxima at midlatitudes (e.g., Mannion et al. 2014), are difficult to interpret, given that nearly all dinosaur species are known only from the locality where they were initially discovered (Dodson 1990) and that sampling is massively biased in favor of midlatitudes (Taylor 2008; and the map in Hunt 2010). The above-cited flattened LDG in early Cenozoic mammals across North America appears to be more robust than the dinosaurian trend, as it is confined to a more evenly sampled region (Marcot et al. 2016) and is centered over a midlatitude portion of the LDG likely to be nearly flat in a greenhouse-climate world (see, e.g., Archibald et al. [2010, 2013] on low seasonality at high Eocene latitudes).

Comparative analyses among clades will require improved methods of integrating fossil data with molecular phylogenies and of developing models for clades having sparser fossil records than marine bivalves—both of these active areas of research. This integration of neontological and paleontological data, promoted by high-throughput genetic methods and the next generation of evolutionary models, will open the door to an enormous range of basic questions; we can mention only a few here. Comparative historical analysis among regions, particularly along longitudinal transects, will help determine when the significant diversity differences among tropical regions were established—an exercise that requires some knowledge of the extinct components of regional biotas. For example, the timing of the massive diversity differences between the marine biotas of the tropical West Pacific and the Caribbean (see fig. 2) is poorly known, owing to the aforementioned fossil-sampling biases (also Johnson et al. 2015). For a given region, the phylogenetic structure of the OTT dynamic may vary among clades or at different times (e.g., according to the steepness of the climate gradient and thus the sharpness of the tropical-temperate boundary). Strict monophyly of the OTT component of clades appears unlikely in clades having large numbers of bridge species (i.e., species straddling the tropical-temperate boundary; Jablonski et al. 2013) but should be stronger as the frequency of bridge species declines, as appears to occur in at least some terrestrial

lineages (e.g., Fine 2015). Accordingly, certain plant clades are highly polyphyletic in their OTT patterns, although a strong phylogenetic signal prevails at higher levels (Donoghue and Edwards 2014).

Still uncertain is whether bivalves or other groups vary strongly in their per-taxon origination with latitude, a question related to diversity-dependent dynamics. Such latitudinal variation appears likely for bivalves given the paucity of young taxa at high latitudes, whether arising in situ or arriving via range expansion, but definitive tests require robust estimates of standing diversity along the LDG through multiple climate cycles. Such estimates, at least in relative terms, can be obtained with some confidence in the well-sampled temperate zones but are more difficult for the crucial but undersampled tropics, particularly in the global diversity maximum in the tropical West Pacific (see Valentine et al. 2013; Vilhena and Smith 2013). On coarser, Phanerozoic timescales, for all marine invertebrates, Kiessling et al. (2010) estimated tropical diversities and found greater per-taxon genus origination in the tropics relative to higher latitudes, and Jablonski (1993, 2005; see also Martin et al. 2007) found excess origination of higher taxa (orders) in the tropics relative to sampling at the species level. These results are consistent with the hypothesis that the tropics have higher per-taxon origination rates in the ocean at least, but more detailed analyses—almost certainly requiring fossil data, given the need to include extinct taxa in the denominator of the equation—are needed to resolve this question.

Finally, we also know little about why some taxa exhibit such strong OTT dynamics while many others do not. In marked contrast to plants, bivalves lack strong phylogenetic patterns in clade success or failure in permanently expanding OTT. Key factors promoting the OTT dynamic in plants, such as frost tolerance, evidently fall more strongly along phylogenetic lines than the analogous traits in bivalves (see Jablonski et al. 2013; see also Fine 2015). One pattern that emerges in bivalves is the tendency for genera with higher diversification rates to contribute disproportionately to the OTT dynamic, suggesting that "speciation pressure" increases the probability that a taxon successfully crosses the tropical-temperate boundary (Jablonski et al. 2013; Tomasovych et al. 2016). In fact, speciation pressure may promote the crossing of major climate boundaries in either direction. For example, the bird clades that evidently invaded the New World tropics from the Northern Hemisphere (i.e., inverting the OTT dynamic; see Kennedy et al. 2014; Claramunt and Cracraft 2015) also show higher diversification rates than clades restricted to either region (Tomasovych et al. 2016). Thus, in groups as disparate as birds and bivalves, genera that cross the tropical-temperate divide have more species in the tropics than do tropical endemics and have more extratropical species than do genera restricted to extratropical regions. New generalizations will continue to emerge from comparative analyses at these large spatial and phylogenetic scales.

Conclusion

We have argued here that a model system that provides spatially explicit historical data yields compelling evidence for both in situ environmental control and interregional dynamics in large-scale diversity patterns, and it would be fascinating to determine whether the two sides are weighted equally across a wide variety of clades and settings. Extending a new set of phylogenetic models for diversification to include in situ climate and habitat components and the spatial dynamics described here remains a challenge but is essential for breaking down the dichotomy that is the focus of this article. The arguments presented here suggest a new generation of large-scale questions about biodiversity, which can best be answered by the integration of paleo- and neontological approaches. Given a synthetic view of today's LDG shape as the product of origination, extinction, and past geographic shifts of taxa, all of those variables might differ among clades, functional groups, and land masses or ocean basins, even when the first-order gradient is similar among those groups and biomes. Furthermore, as implied by figure 1, these variables are not necessarily independent. For example, the evolution of new taxa in one area can fuel dispersal into an adjacent region through post-speciation range expansion (Jablonski et al. 2006). Similarly, changing climate or habitat characteristics in one area (an in situ dynamic) could promote range expansion into the area of species from adjacent regions. Owing to such interdependence, failure to take into account the dispersal parameter can, in some cases, even affect the reliability of diversification rate estimates (Roy and Goldberg 2007). Neither the data most readily available for extant species nor the fossil record fully capture the interplay of these factors on their own. But integrating spatially explicit fossil data with modern biogeography and phylogeny can provide a powerful vehicle for testing hypotheses and generating new ones. This combined approach will be the most powerful not just for a deeper understanding of past and present biodiversity but for anticipating biotic changes in the face of accelerating global change.

Synthesis of interactions among mechanisms may be fundamental for understanding many of the most dramatic biodiversity patterns. The search for unitary mechanisms is a valuable means of sharpening hypotheses and discarding the weaker ones, but the most extreme patterns may be generated by diverse, mutually reinforcing drivers (as also noted by, e.g., Gaston [2000]). In this light, the West Pacific Coral Triangle is probably the global marine hotspot because it is a "perfect storm" for biodiversity, combining an

array of in situ factors, including warm temperatures, low seasonality, a vast area, a wide range of habitat types (reefs and mangroves to lagoons and open shelves), a complex island-mainland structure, and intense biotic interactions, with a strong spatial dynamic involving the influx of taxa from other tropical regions (e.g., Leprieur et al. 2016). The end-Permian mass extinction was by far the most severe in the Phanerozoic because many mutually reinforcing factors conspired to draw down diversity, most likely with a volcanic trigger (Payne and Clapham 2012). The Cambrian explosion was the most dramatic phenotypic diversification of multicellular organisms because development, ecology, and such external cues as oxygen levels successively fell into place in a mutually reinforcing fashion (Erwin and Valentine 2013). Insects are the most diverse metazoan clade because they have many attributes promoting high speciation and low extinction rates (Mayhew 2007), and several major plant radiations, including Bromeliaceae and Orchidaceae, evidently involved the confluence of multiple innovations and environmental shifts (Donoghue and Sanderson 2015). Such multifactorial explanations do not mean that we cannot rank drivers in particular cases, but they indicate that comparative analysis and synthesis can yield new insights—why the end-Cretaceous or late Devonian extinctions were less severe than the end-Permian extinction, why the recovery from the end-Permian extinction was less dramatic than the Cambrian explosion, why the diversification of squamates or birds was less dramatic than that of insects—and new approaches to integrating fossil and present-day data are likely to be key to our understanding.

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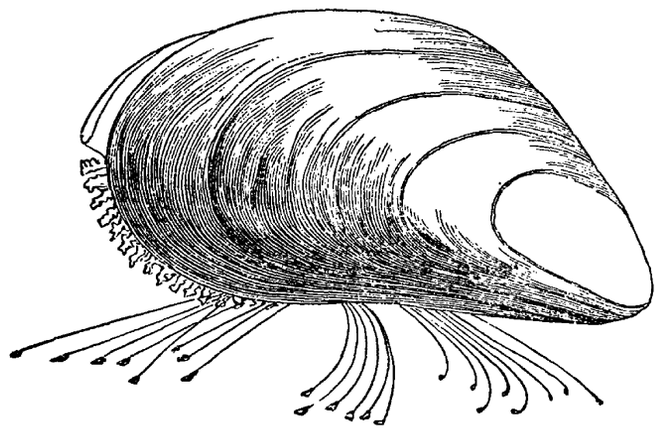

The common mussel (*Mytilus edulis*). From "Life Histories of the Mollusca" by A. S. Packard Jr. (*The American Naturalist*, 1875, 9:282–307).