Review

Generation of Earth's First-Order Biodiversity Pattern

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Abstract

The first-order biodiversity pattern on Earth today and at least as far back as the Paleozoic is the latitudinal diversity gradient (LDG), a decrease in richness of species and higher taxa from the equator to the poles. LDGs are produced by geographic trends in origination, extinction, and dispersal over evolutionary timescales, so that analyses of static patterns will be insufficient to reveal underlying processes. The fossil record of marine bivalve genera, a model system for the analysis of biodiversity dynamics over large temporal and spatial scales, shows that an origination and range-expansion gradient plays a major role in generating the LDG. Peak origination rates and peak diversities fall within the tropics, with range expansion out of the tropics the predominant spatial dynamic thereafter. The origination-diversity link occurs even in a "contrarian" group whose diversity peaks at midlatitudes, an exception proving the rule that spatial variations in origination are key to latitudinal diversity patterns. Extinction rates are lower in polar latitudes ($\geq 60°$) than in temperate zones and thus cannot create the observed gradient alone. They may, however, help to explain why origination and immigration are evidently damped in higher latitudes. We suggest that species require more resources in higher latitudes, for the seasonality of primary productivity increases by more than an order of magnitude from equatorial to polar regions. Higher-latitude species are generalists that, unlike potential immigrants, are adapted to garner the large share of resources required for incumbency in those regions. When resources are opened up by extinctions, lineages spread chiefly poleward and chiefly through speciation. Key Words: Latitudinal diversity gradients—Origination—Extinction—Evolution—Distribution of complex life. Astrobiology 9, 113–124.

1. Introduction

COMPLEX LIFE ON EARTH is deployed neither randomly nor evenly over the planet's surface. The principal global pattern of biodiversity is the latitudinal diversity gradient (LDG), with the richest biotas (in terms of diversity, morphology, or functional groups) in low latitudes grading poleward to the least rich, for all major groups of multicellular organisms on land and in the sea (Ricklefs and Schluter, 1993; Rosenzweig, 1995; Willig *et al.*, 2003; Hillebrand, 2004) (Fig. 1). For animals, the LDG is observed at all taxonomic levels below phyla, though a few groups (which we have termed "contrarians") show irregular or even reverse gradients (*e.g.*, Kindlmann *et al.*, 2007; Krug et al., 2007). The LDG is an ancient feature, detected throughout the fossil record of complex life (Crame, 2000a, 2002; Novack-Gottshall and Miller, 2003; Fitzgerald and Carlson, 2006; Krug and Patzkowsky, 2007; Powell, 2007; Al-

roy *et al.*, 2008), though its slope has varied and may even have been temporarily disrupted by major extinctions (Jablonski, 2005b) or climatic fluctuations (Powell, 2007). A pattern so pervasive, among taxa and across geological time, implies a fundamental property of complex life with a unifying suite of physical, ecological, or evolutionary processes at its core. Understanding the formation of LDGs will, therefore, not only add insight into the factors underlying the evolution and distribution of advanced life on Earth but also may provide the key to understanding the planetary conditions on which complex life can evolve and diversify.

2. The Search for a Consensus

The LDG was the first diversity pattern identified by biologists, but as Hawkins (2001) noted, "attempts to understand the gradient continue, although the number of 'expla-

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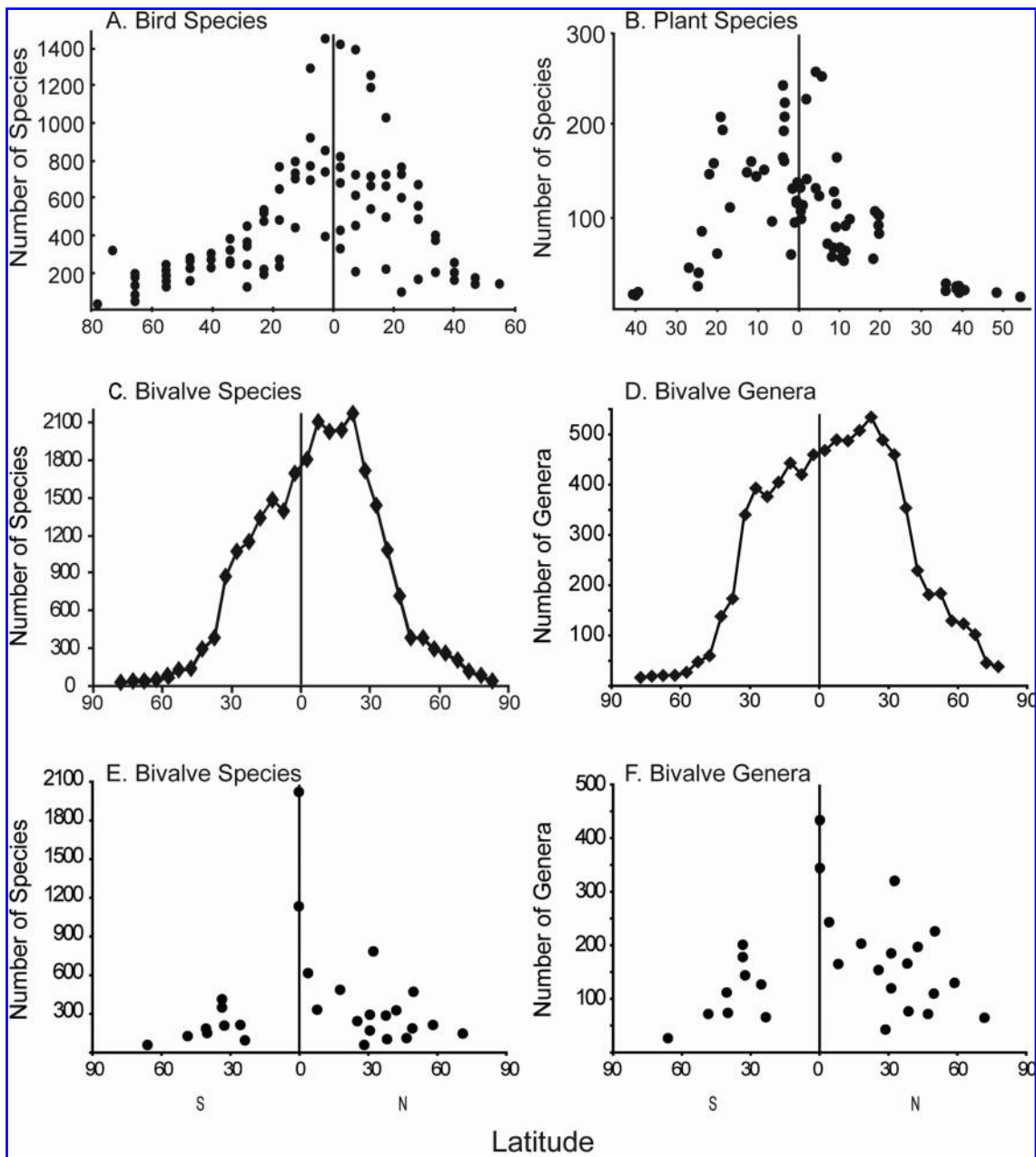
FIG. 1. Latitudinal diversity gradients for various taxonomic groups. (**A**) Bird diversity calculated for grid cells from the New World (redrawn from Gaston, 2000a); (**B**) Plant diversity from lowland forests, calculated for 1000 m² samples (redrawn from Gentry, 1988). (**C**) Global species richness for marine bivalves, calculated for 5° latitudinal bins; (**D**) Global genus diversity for marine bivalves, calculated for 5° latitudinal bins. (**E**) Bivalve species richness within marine biogeographic provinces. (**F**) Bivalve genus richness within biogeographic provinces. Though biogeographic provinces vary in size, there is no correlation between the available coastline and the diversity within a province (for genera, Spearman's rho = 0.18, p = 0.37; for species, Spearman's rho = 0.26, p = 0.29). Vertical line in each panel marks the equator.

nations' is increasing rapidly, with over 30 hypotheses in the literature and new ones appearing almost yearly." Indeed, despite 150 years of speculation, investigation, and debate, the factors underlying LDG formation remain poorly understood or at least poorly agreed upon. Studies of LDGs have traditionally focused on ecological factors, including correlations between diversity and various climate parameters (Jablonski *et al.*, 2000; Roy *et al.*, 2000), habitat area or complexity (Rosenzweig, 1995; Davies *et al.*, 2007), or species

ranges (Maurer and Nott, 1998; Roy *et al.*, 2001). None of these factors, evoked singly or combined to explain gradients in various taxa, has gained general acceptance. Biodiversity can be increased only by originations, lowered by extinctions, or altered regionally by immigration or emigration, and so the LDG must be controlled, over the long run, by latitudinal variations in these variables (Hawkins and Porter, 2003; Cardillo *et al.*, 2005; Evans and Gaston, 2005; Allen and Gilooly, 2006; Jablonski *et al.*, 2006; Mittelbach *et al.*, 2007;

Roy and Goldberg, 2007; Arita and Vazquez-Dominguez, 2008; Reaka *et al.*, 2008). Thus, a crucial step in understanding the LDG involves determining the relative importance of these factors and how they are regulated at large spatial scales.

Latitudinal diversity gradients have typically been viewed as deriving from a balance between *in situ* origination and extinction, with tropical diversity maxima produced either by high tropical origination rates (the classic tropics-as-cradle hypothesis) or low tropical extinction rates (the tropics-as-museum hypothesis) (Stebbins, 1974). Analyses confined to this stark dichotomy have produced conflicting results. For instance, recent work in which bird phylogenies were used has suggested that increased high-latitude extinction reduces diversity there, which overwhelms spatial patterns in origination (Gaston and Blackburn, 1996; Gaston, 2000b; Hawkins *et al.*, 2006, 2007; Weir and Schluter, 2007; Jansson and Davies, 2008; but see Martin and Tewksbury, 2008). Studies on other taxa, however, have suggested increased origination rates in tropical climate zones, inferred from phylogenies, fossil evidence, or the geological-age distribution of the faunas (Stehli *et al.*, 1969; Flessa and Jablonski, 1996; Williams, 2007), even in lineages that have migrated into the tropics following their origination elsewhere (Wiens *et al.*, 2006).

Recent research efforts on modern LDGs generally determine origination and extinction rates from phylogenetic analyses of extant taxa for which a robust fossil record is lacking (Gaston and Blackburn, 1996; Hawkins *et al.*, 2006; Wiens *et al.*, 2006; Hawkins *et al.*, 2007; Mittelbach *et al.*, 2007; Weir and Schluter, 2007; Wiens, 2007; Jansson and Davies, 2008). However, phylogenies cannot reliably pinpoint the location of first or last appearance, or the direction of subsequent spread of a taxon, and this critical historical component must therefore be inferred from modern geographic distributions of sister taxa. This may be problematic, considering the sometimes complex history of lineages, which involves climate swings, extinction events, and tectonically driven continental shifts. Further, phylogenies based only on extant taxa can only directly assess net diversification rates, rather than decompose those rates into the origination and extinction components that are essential to understanding the underlying processes (Mittelbach *et al.*, 2007). Progress is being made on modeling approaches to this problem, but assumptions are strong and uncertainties large (Ricklefs, 2007). Such analyses can also overlook the sometimes large number of now-extinct clades that may have influenced the distribution or diversification of extant taxa. Additionally, such models do not take into account the role of dispersal, which can affect retroactive rate calculations (Roy and Goldberg, 2007).

The fossil record, if analyzed carefully, can provide a direct window into the spatial behavior of evolutionary lineages, as well as information on the extinct progenitors of modern taxa. However, variable spatial and temporal preservation of fossils leaves only a portion of ancient ecosystems available for analysis, and this portion is even more severely biased toward temperate regions than are present-day marine samples (Allison and Briggs, 1993; Jackson and Johnson, 2001; Bush and Bambach, 2004; Jablonski *et al.*, 2006; Valentine *et al.*, 2006, see below). Additionally, the preservation of fossils makes consistent, reliable identification to the species

level difficult, so that large-scale analyses are generally performed at the next highest, genus level. Both biological and paleontological data, therefore, have unique advantages and limitations, and definitive results are best obtained by analyzing both simultaneously.

3. A Model System

We have studied the LDG in marine environments by integrating biological and paleontological data to produce a dynamic evolutionary model on the formation of LDGs (Jablonski *et al.*, 2006; Krug *et al.*, 2007, 2008; Valentine *et al.*, 2008). We use Bivalvia (Mollusca) as a model taxon because it is among the most diverse of marine classes (~3000 living and fossil genera), occurs at all latitudes and depths, has a rich fossil record (Valentine, 1989; Kidwell, 2005; Valentine *et al.*, 2006), and is comparatively well known taxonomically and biogeographically, both as fossils and in the living fauna (Crame, 2000a, 2000b; Giribet and Wheeler, 2002; Jablonski *et al.*, 2003; Bieler and Mikkelsen, 2006; Valentine *et al.*, 2006). Additionally, bivalve diversity patterns today and through the Cenozoic correspond closely to those of other major marine clades, both spatially and temporally (Bellwood and Hughes, 2001; Mora *et al.*, 2003; Bellwood *et al.*, 2005; Briggs, 2007; Reaka *et al.*, 2008; Williams and Duda, 2008), so we expect results for bivalves to be generally applicable to other modern marine clades, though certainly some will deviate. The marine bivalves of the continental shelves have a strong LDG, whether binned by global latitudinal bins (Fig. 1C, 1D) or by biogeographic provinces (Fig. 1 E, 1F), though the former captures the spatial differentiation among localities and regions and, therefore, provides a more accurate global picture of the latitudinal decline in richness (tropical biotas differ far more strongly among coasts than do polar ones). Because tropical environments are undersampled relative to higher latitudes for mollusks (*e.g.*, Bouchet, 1997; Bouchet *et al.*, 2002) and other marine groups (Mora *et al.*, 2008), the true LDG is probably even steeper than presently known.

As already noted, the fossil record is less complete at each lower taxonomic level, so we generally work at the level of genera and subgenera (hereafter simply genera), as experience has led us to conclude that (1) data at the family level are too coarse to permit detection of important macroevolutionary dynamics; (2) the fossil record of faunas at the species level, where the dynamics originate, can be too incomplete for oceanic or global analyses (~80% of bivalve genera that inhabit intertidal and shelf depths today have a fossil record, whereas <50% of species occur as fossils, though that number is much higher in well-studied regions); and (3) species-level data are subject to severe biases from uneven taxonomic treatments and differences in sampling methods and intensities. Our modern biogeographic database of 854 living genera (out of 1293 known) and 5132 species (out of ~11,000) currently contains 332 localities and 28,264 occurrences (here defined as the presence of a species in a locality). These numbers encompass all or most of the genera in each of the major branches of the bivalve evolutionary tree; we aim to have complete coverage of shelf-depth marine bivalves in the near future, except for a subset of very small-bodied forms (~120 genera) that remain poorly known and undersampled by modern standards. In addition to pinning occurrences to specific locations or small regions, we assign occurrences to a

three-bin model of climate zones (tropical, temperate, and polar) on the basis of the physical features of hydrographic compartments as described by Longhurst (1998), with a few minor modifications following Spalding *et al*. (2007). The assignments of localities to climate zones apply only to the modern fauna, as the climatic shifts of the Cenozoic certainly altered these associations through time.

To trace the roots of the modern deployment of biodiversity, we (1) compiled the age and location of the oldest known fossil occurrences of each of the living genera and (2) standardized the taxonomy of fossil marine genera of Bivalvia reported in the fossil record of the last 11 million years, which encompasses three time bins—Late Miocene, Pliocene, and Pleistocene (as employed in Jablonski *et al*., 2003, 2006; Valentine *et al*., 2006; Krug *et al*., 2007). The location of the first occurrence of each genus was determined by a search of the primary literature for the oldest known specimens of a given genus. These locations were then integrated into a highly revised version of Sepkoski's database of marine animal genera (Sepkoski, 2002), which originally listed 2873 bivalve genera. To date, we have made 1334 changes to Sepkoski (2002), which include minor adjustments of range endpoints, significant stratigraphic range extensions and contractions, and the addition of newly described (or newly recognized, via our own work or others) genera and deletion of genera now synonymized with other genera in the database. Six hundred and twenty of these changes are Cenozoic, 517 Mesozoic, and 197 Paleozoic. These quantities are roughly proportional to the number of genera recorded from each Era. [An Excel spreadsheet documenting the age and location of first occurrences of marine bivalve genera is posted in association with Krug *et al*. (2007) at http://geosci.uchicago.edu/people/jablonski.shtml. An earlier version is posted at the same website in association with Jablonski *et al*. (2003).]

To evaluate biases in the fossil record, we used the proportion of living genera with a known fossil record within each bivalve family (Valentine *et al*., 2006) as a first-order sampling gauge. This procedure cannot, however, correct for spatial variations in sampling and preservation, which are strongly biased against tropical regions, particularly the Indo-West Pacific. As a rough assessment of this bias, we used the *Paleobiology Database*, a massive, community-wide compilation of paleontological data (paleodb.org), as an approximation of the general distribution of data from the recent paleontological literature. We downloaded all marine bivalve records from the Cenozoic 6 time bin, which represents roughly 10 million years of geological time, including the Late Miocene, Pliocene, and Pleistocene (downloaded August 19, 2008). As with records of extant species, the great preponderance of fossil bivalve occurrences for this time interval are derived from Northern Hemisphere extratropical localities (Fig. 2). The West Pacific has been the primary global diversity center since the Miocene (Vermeij, 2001; Crame and Rosen, 2002; Renema *et al*., 2008; Williams and Duda, 2008), which exceeds the New World tropics in genus diversity by at least a factor of 2 in our data, but the Western Atlantic tropics are much better sampled (though, even along this coast, extratropical sampling exceeds that of the tropics; see Fig. 2). Polar zones are also undersampled, but the well-known taxonomic homogeneity of polar faunas, particularly at the genus level, indicates that further sam-
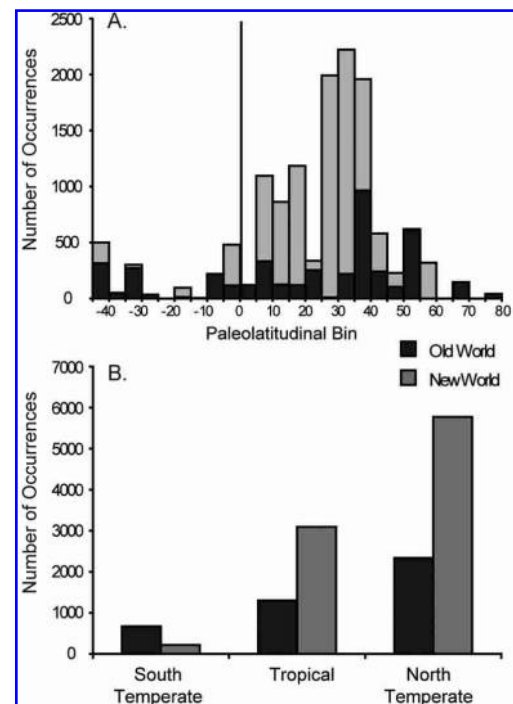

FIG. 2. Sampling biases and latitude. (**A**) Number of bivalve occurrences in 5° paleolatitudinal bins downloaded from the Cenozoic 6 time bin (Late Miocene, Pliocene, Pleistocene) of the *Paleobiology Database* (paleodb.org). Vertical line marks the equator. (**B**) Number of bivalve occurrences within south temperate, tropical, and north temperate climate bins from the same time period. Paleolatitudes >25° were considered temperate.

pling will not qualitatively shift diversity trends. The Southern Hemisphere is generally less sampled than the Northern Hemisphere in both tropical and extratropical bins (Fig. 2), but these sampling deficiencies are unlikely to alter the results presented below, as we focus on global climate zones.

This latitudinal sampling bias reflects a real deficiency in the relative paleontological sampling of tropical versus extratropical zones. A preliminary analysis of references not yet in the *Paleobiology Database* suggests that the gap in sampling is actually much wider than currently recorded there. An intensive literature search and taxonomic standardization for Indonesia, which Beu (2005) noted as the richest and most extensive paleontological sample of the entire Indo-West Pacific core of marine molluscan diversity, added only 137 Late Miocene and 464 Pliocene bivalve occurrences (and over 150 genera) to the region. This represents fewer occurrences than would be added to temperate regions by only a single study from the Belgian Pliocene [630 additional occurrences (Marquet, 2002, 2005)], two studies from the late Neogene of central Japan [718 occurrences (Tomida, 1996; Ozawa *et al*., 1998)], or even Wood's classic monograph on the Pliocene-Pleistocene of southern England [626 occurrences (Wood, 1874)]. These extratropical sources add far fewer genera to the total recorded from these areas than do the occurrences from Indonesia, yet they represent only a minute fraction of the material collected, identified, and published from these regions.

Variations in sampling intensity have long been known as a source of error in estimating diversity from the fossil record, and sampling standardization methods are being developed to account for these and other biases (Miller and Foote, 1996; Alroy, 2000; Alroy *et al.*, 2001; Bush and Bambach, 2004; Bush *et al.*, 2004; Alroy *et al.*, 2008). Although the spatial and environmental distribution of global occurrences are biased, the data exist, through literature sources and museum collections, to produce a robust and accurate assessment of the evolutionary and spatial dynamics leading up to the present day. Presently, even our qualitative knowledge of the direction of the sampling bias (above) allows us to infer that the results presented below are robust, as they trend in the opposite direction to the principal bias toward better extratropical sampling.

4. Dynamics of Global Biodiversity

4.1. Genus originations

When the first occurrences of genera are plotted against the preservation quality of their families, we find that the genera within well-preserved families (with >75% of their genera known as fossils) preferentially first appear in the tropics (Fig. 3A), which significantly exceeds extratropical first appearances for each time bin. This pattern occurs in each time bin over the past 11 million years (Fig. 3B–3D) and for the study interval as a whole, which contains 108 tropical and 45 extratropical first occurrences. This indicates that the pattern is robust to the placement of individual records within time bins ($p < 3.7e\text{-}07$, exact binomial test). The poor tropical sampling relative to other climate zones implies that the fraction of tropical first occurrences is an underestimate

of the true value, so we conclude that tropical originations far outstrip extratropical ones and only a few, if any, genera originating extratropically have entered the tropics. We have dubbed the scenario of high tropical originations and subsequent expansion to higher latitudes the out-of-the-tropics dynamic (Jablonski *et al.*, 2006). As expected from such a dynamic, genera with tropical occurrences make up about 75% of the fauna at all extratropical latitudes, and the median age of genera increases poleward (Fig. 4A), which also suggests that origination rates decrease with latitude (see Foote, 2001). We thus hypothesize that, over the past 11 million years at least, origination rates were highest in the tropics for Bivalvia, with origination thus positively correlated with diversity. However, sampling is not yet adequate for a robust assessment of per-taxon origination rates: the tropics might be more prolific in the generation of novelty per speciation event, or it might simply produce so many novel genera because of its larger species pool.

We tested the relation between origination and diversity by using a contrarian clade (the order Anomalodesmata) whose peak diversity is in the temperate zone, near 35°, with a reverse LDG into lower latitudes and a normal LDG toward high latitudes (Krug *et al.*, 2007). The youngest median age (equal to the reciprocal of origination rate) of the anomalodesmatan genera also occurs near 35° (Fig. 4B). Regions of peak diversity, therefore, correspond geographically to regions of minimum ages and peak origination regardless of latitude, which attests to the role of origination in producing geographic diversity patterns with or without standard LDGs. Remarkably, the anomalodesmatans fit closely into the quantitative relationship seen for the normal-gradient bivalve groups between the steepness of the LDG and the pro-
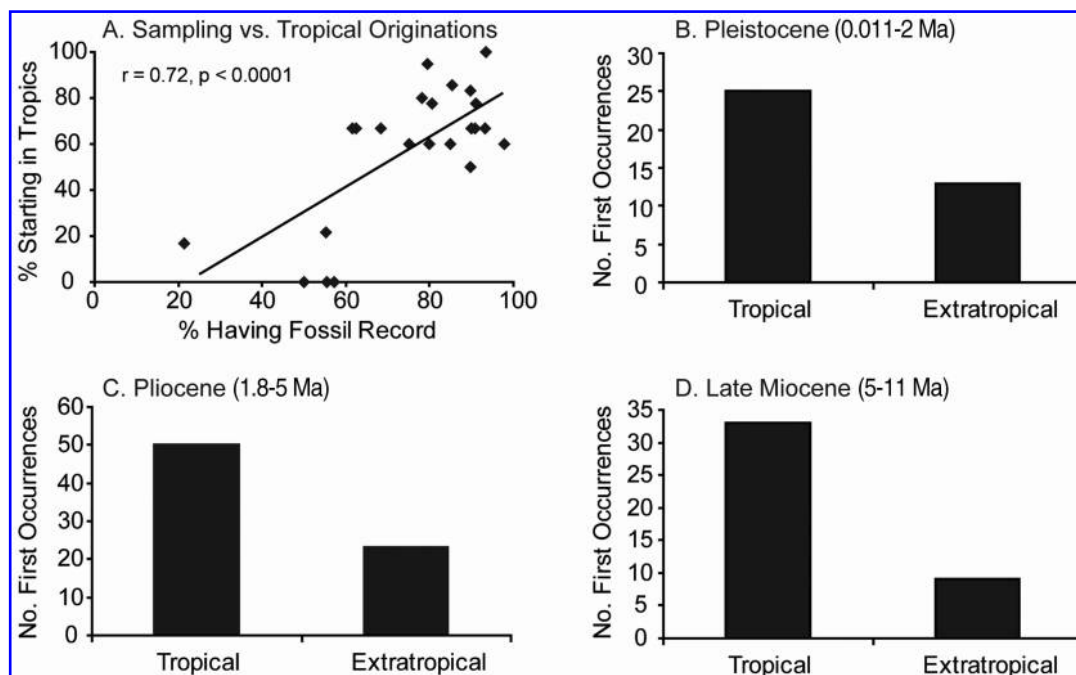

FIG. 3. (**A**) Significant correlation between the proportion of genera preserved within a family and the proportion of genera originating in the tropics ($p = 0.007$, Spearman's rank test). (**B**) Numbers of Pleistocene tropical and extratropical originations; (**C**) Numbers of Pliocene tropical and extratropical originations; (**D**) Numbers of Late Miocene tropical and extratropical originations. After Jablonski *et al.* (2006).
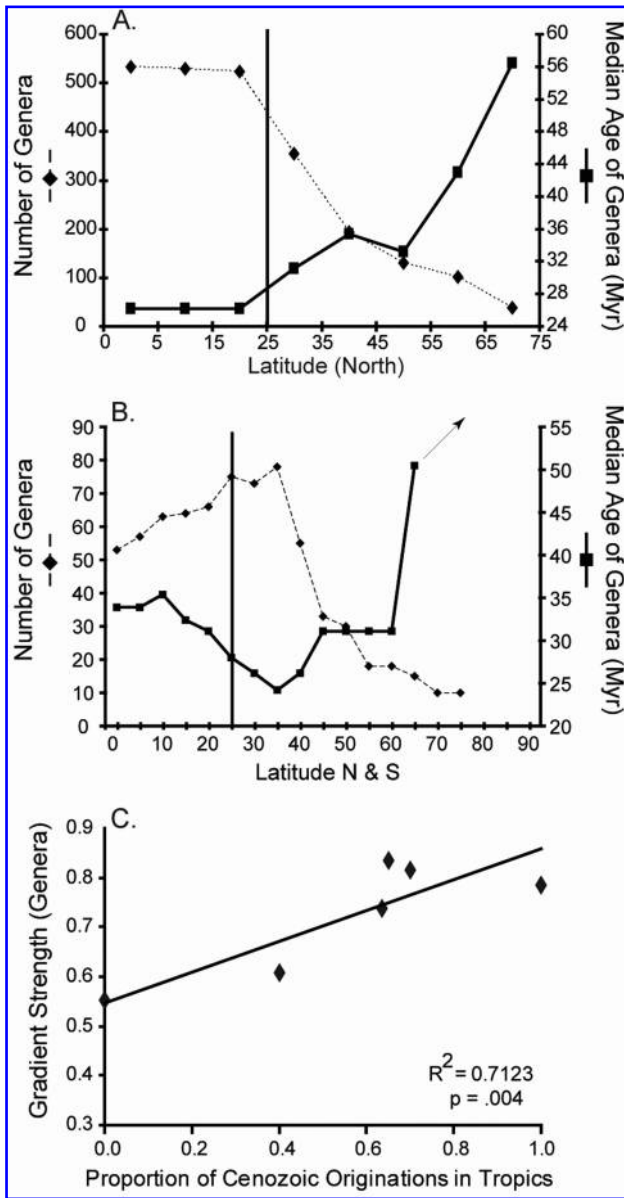
FIG. 4. Latitudinal trends in diversity and median age of genera for (**A**) all marine bivalves (after Jablonski *et al*., 2006; Valentine *et al*., 2008) and (**B**) the contrarian bivalve clade Anomalodesmata (from Krug *et al*., 2007). (**C**) LDG steepness today vs. proportion of tropical originations during the Cenozoic (0–65 Ma) for marine bivalve orders (from Krug *et al*., 2007).

portion of genera originating in the tropics (Fig. 4C). The age distribution of anomalodesmatans within the temperate zone conforms to that of the closely related, standard-LDG veneroids, but is shifted to significantly greater ages in the tropics, which suggests that lower tropical diversities in the contrarian clade result from damped tropical originations rather than heightened temperate diversification. The loss of only one tropical anomalodesmatan genus and six genera in the normal-LDG Veneroida over the past 11 million years corroborates the view that differential extinction is not the primary factor in shaping the contrarian trend. The reasons behind the anomalodesmatans' damped tropical diversifica-

tion are unclear but may involve their developmental system (a low-fecundity, low-dispersal mode), which is unusual for bivalve clades and proportionately more common in high latitudes (Jablonski and Lutz, 1983; Laptikhovsky, 2006), and their low activity rates (Morley *et al*., 2007) relative to other bivalve groups.

4.2. Genus extinctions

Miocene polar faunas are not well represented in the fossil record, so we have compared extinctions for each of the three climate zones within two time bins, the Pliocene and Pleistocene (*i.e*., about the last 5 million years) (Valentine *et al*., 2008). Data are not yet completely available globally but do allow for a preliminary analysis of regional extinction rates of the Northern Hemisphere. Both local and total extinction were greatest in the temperate zone, which produces a hump-shaped distribution of extinction with latitude (Fig. 5). This marked discordance with the LDG indicates that the low diversity at the poles represents mainly a dearth of origination (and, as discussed below, a dearth of invasion) rather than maximal extinction, though little is known about polar extinction intensities prior to 5 Ma (mega annum). The climate changes through this time period, especially during the glacial-interglacial climate swings, were responsible for many geographic range shifts, which are well documented in temperate marine faunas around the world and involved hundreds of kilometers for some species (Valentine and Jablonski, 1993; Beu, 2004; and see Jackson and Williams, 2004 for similar dynamics on land). Marine temperature variability is greatest at present in temperate latitudes, and the glacial-interglacial climate swings were also most severe in temperate latitudes. It is plausible to attribute the higher temperate extinctions to the more extreme climatic variability there, though further testing is needed.

4.3. Range expansion

An underlying assumption of virtually all analyses of the latitudinal gradient is that taxa remain in their climate zone of origin (Blackburn and Gaston, 1996; Flessa and Jablonski, 1996; Cardillo, 1999; Cardillo *et al*., 2005). The fossil record,
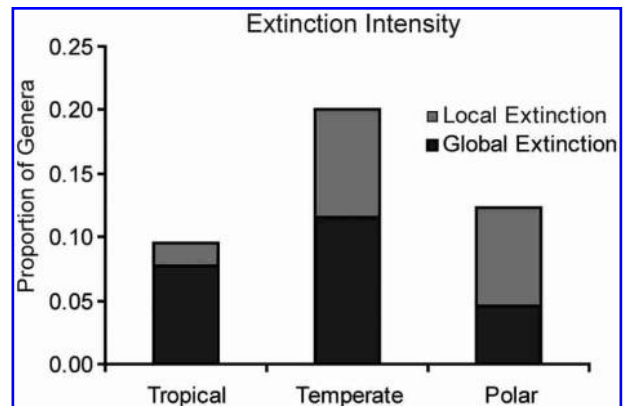

FIG. 5. Preliminary estimates of local and global genus extinction intensity in tropical, north temperate, and north polar regions for the Pliocene and Pleistocene (0–5 Ma), after Valentine *et al*. (2008).

however, demonstrates that taxa often change their spatial distributions over time, either through range shifts that track climatic parameters (Valentine and Jablonski, 1993; Jackson and Williams, 2004) or through range expansions promoted by evolutionary innovations, ecospace opened by extinctions, and the creation of new dispersal routes (Patzkowsky and Holland, 1996; Miller, 1997; Foote, 2007; Holland and Patzkowsky, 2007). Over the last 11 million years, bivalve genus range shifts have been predominantly from tropical to extratropical regions, and those genera expanding their ranges tended to maintain their tropical presence, building diversity in this region (Jablonski *et al.*, 2006). Thus, rather than regional diversity being driven solely by *in situ* diversification, range expansion seems to be a fundamental and predictable process in LDG formation.

The appearance of a genus in a region from which it has been absent requires the entry of at least one of its species. Range expansion of marine species has been studied mainly from the standpoint of island biogeography, in which long-distance transport between islands is commonly required and propagules such as long-lived planktotrophic larvae are important elements of invasion success (*e.g.*, Paulay and Meyer, 2006). At present and throughout the late Cenozoic, however, the north-south alignment of most continental shelves has provided broad corridors for migration across latitudes by simple spreading, when ecological factors that limit geographic range, such as temperature, are shifted (Valentine and Jablonski, 1993; Gaylord and Gaines, 2000). Thus, the LDG is unlikely to be significantly affected by long-distance barriers around continental shelves; in fact, even in the central Pacific, where shallow-water habitats are commonly scattered among distant islands, the LDG is quite strong and symmetrical about the equator (Connolly *et al.*, 2003).

The shape of the LDG may, however, change during major climatic swings, such as the glacial-interglacial shifts of the Pleistocene. Species and genera are known to track isotherms during climatic shifts, so that taxa that expanded poleward during greenhouse conditions (Addicott, 1970) will subsequently contract their ranges with the onset of glaciation (Roy *et al.*, 1995). Though this will affect the steepness of the LDG, it does not in itself provide a mechanism for the formation of the LDG or for lineages to become established in new climate zones (Valentine *et al.*, 2008).

In general, introduced species tend to spread rapidly at first but then slow down so as to suggest negative feedbacks (review in Arim *et al.*, 2006). A similar dynamic occurs in population growth when limits are placed by density-dependent factors, and it has been suggested that somewhat analogous diversity-dependent factors can also limit the number of species and genera that can be accommodated within a region (Valentine, 1972, 1973; Valentine *et al.*, 2008). Such diversity-limiting factors consist of resources that can be used up by species, such as dependable food and living space, whereas factors that cannot be used up, such as temperature, are diversity independent. Under a model of species diversity dependence, the spreading rate of species, once they have physical access to a region, perhaps owing to a climate change, would be limited by the availability of diversity-dependent resources in the adjoining or invaded region to sustain them—the diversity accommodation space of the region. Of course, as a species spreads, its genus

spreads as well, so long as it is not already represented in the invaded region. Models that incorporate macroevolutionary dynamics in a spatially explicit context can greatly enhance our understanding of the interplay between diversity-dependent variables and spreading rates.

4.4. Speciation and genus biogeography

As noted above, the LDG must involve some combination of range expansion and *in situ* diversification at both the genus and species levels. To investigate the species dynamics of the LDG further, we determined the ratio of bivalve species to genera (S/G ratio) in each 5° latitudinal bin and in climate zones, globally (Fig. 6). S/G is expected to drop with latitude because regions with fewer species should, mathematically, always have lower S/G ratios (Simberloff, 1970). However, the S/G ratios for both tropical and polar latitudinal bins significantly exceed the null expectation, which means that fewer genera are present in these regions than expected given the species richness there (see Krug *et al.*, 2008, for a more detailed description of the null model).

The decline in S/G, and the significant divergence from the null at high and low latitudes, is not pervasive in bivalves. Genera extending across the entire LDG have more species overall and in each climate zone than do genera endemic to a single climate zone (Table 1), which show no latitudinal or climatic trend in S/G. We hypothesize that the high S/G ratio of the polar zone, which is largely due to cosmopolitan genera that have spread into the region [presumably from the tropics (Goldberg *et al.*, 2005; Roy and Goldberg, 2007)], indicates a link between speciation rate and biogeographical spread. That is, we propose that genera with high speciation potential are more likely to become latitudinally cosmopolitan, a distribution attained primarily by the
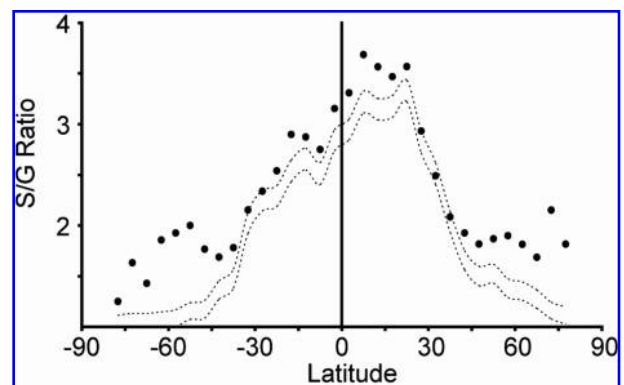
FIG. 6. Species-genus ratios for marine bivalves plotted against latitude (from Krug *et al.*, 2008). Black circles represent the S/G ratio observed in our data. Dashed lines are 95% confidence intervals for the S/G ratio expected under our null model. For the null model, we took the actual latitudinal ranges of species with each 5° bin and randomly assigned them to genera, without replacement, so that each genus retained its original species richness. The S/G ratio from this randomized set was then determined within each 5° latitudinal bin, the process repeated 1000 times, the results averaged, and a standard error calculated. This procedure produced an expected S/G ratio for each bin if the S/G ratio arose from a random distribution of species into genera yet retained the spatial autocorrelation of the dataset.

TABLE 1.   MEAN NUMBER OF SPECIES WITHIN GENERA
OF VARIOUS GEOGRAPHIC RANGE CLASSES
(AFTER KRUG ET AL., 2008)

	N	Tropical	Temperate	Polar
All genera	769	5.1	4.0	2.0
Cosmopolitan genera	95	7.5	5.5	2.2
Warm-water genera	444	5.3	3.6	—
Cold-water genera	33	—	2.7	1.4
Tropical endemics	87	1.54	—	—
Temperate endemics	110	—	1.72	—

Cosmopolitan genera exist in tropical, temperate, and polar climate zones. Warm-water genera exist in tropical and temperate climate zones. Cold-water genera exist in temperate and polar climate zones. Values for cosmopolitan genera in the temperate zones are the average of the Northern and Southern Hemispheres.

splitting off of new species across environmental barriers of varying magnitudes. One test for this idea is to examine cosmopolitan genera that have species that range from tropical to polar zones, rather than having shorter-ranging species arrayed along latitudes; our hypothesis implies that these genera with cosmopolitan species should be relatively species poor.

5. Discussion: an Integrated View of Latitudinal Diversity Dynamics

5.1. Summary of latitudinal dynamics.

The dynamics of the bivalve LDG are thus coming into focus. A high tropical origination rate both of genera and of species, together with the tropical retention of those lineages (as indicated by their age-frequency distributions and low tropical extinction rate), produces a strong diversity peak in low latitudes. Species spread poleward, perhaps under the influence of climate fluctuations, and carry their genera along. Genera that speciate more often tend to be the genera that extend their ranges across the entire LDG, which produces on average not only more species within each latitudinal bin or climate zone but also invading populations that cross climatic barriers to invade new climate zones and diversify there. New bivalve genera are also produced in temperate zones; but, considering sampling biases, these probably comprise much less than one quarter of the generic fauna there. Connections of the invading populations with their parent species may often be severed by additional climate change, with climate fluctuations thus pumping lineages to higher latitudes (Valentine, 1968), though other ecological factors may also be involved. At any rate, the environmental variability of temperate latitudes is associated with higher extinctions, which frees resources, and new "replacement" lineages seem to be mostly recruited from the exceedingly rich tropical faunas rather than evolving *in situ*. The polar zone fauna has a poor fossil record, especially before the Pliocene, but appears to have been relatively stable generically at least from that epoch on, with a lower extinction rate than in midlatitudes, despite the repeated glaciations (Valentine *et al.*, 2008). Presumably, marine mollusks could persist in deeper water when confronted with surface ice, as they do today on a seasonal basis. This option for persistence in high latitudes is unavailable to terrestrial forms such as plants or birds, which suggests that different spatial dynamics have operated on land and sea, at least over the past few million years (Roy and Goldberg, 2007). The recent recognition of high-latitude terrestrial refugia from glaciation should be assessed from this perspective, however (Rowe *et al.*, 2004; Brubaker *et al.*, 2005; Anderson *et al.*, 2006; Bhagwat and Willis, 2008). The operation of a broadly similar out-of-the-tropics dynamic over the past 250 million years for invertebrate orders ranging from sponges to sea urchins (Jablonski, 1993, 2005a; Martin *et al.*, 2007) suggests that the bivalve patterns reported here are pervasive, at least for complex marine life.

5.2. Incumbency and the LDG

Extinctions aside, it is unclear why origination rates remain low in the high latitudes and why more genera do not expand their ranges into this region. One possibility is that this suppression is due to one or more diversity-dependent factors. One such factor that correlates closely with the LDG is seasonality of primary productivity, which in the sea varies by over an order of magnitude between relatively stable tropical and variable polar latitudes (Valentine *et al.*, 2008). At increasingly higher latitudes, trophic resources become concentrated in increasingly narrow, seasonal windows. Indeed, above the Arctic Circle the Sun does not rise for half the year, and primary productivity becomes very low for a long period. In response to this challenge, many invertebrate species in high-latitude communities tend to be ecologically generalized in some ecological dimensions, such as feeding low in the trophic pyramid, taking a wide variety of prey (some predators even resort to deposit feeding when productivity is low), and occupying a relatively wide range of habitats so that some populations occur in the more favorable localities during generally inclement times. Thus, the incumbent species, adapted to the highly seasonal conditions, require large portions of the habitat in order to persist through inclement seasons or stretches of poor years.

By this hypothesis, the low diversity of high latitudes does not signal a profusion of "empty niches"—available ecological space—but rather indicates a low capacity to accommodate species, which is reflected also in a low genus richness. The high-latitude communities are, therefore, not particularly invasible; extinctions, originations, and immigrations are all low; and the generic assemblage is relatively stable over time. All these attributes are consistent with the fossil record. By contrast, productivity is in general much less seasonal in the tropics, albeit with some local and regional perturbations, and the tropics can therefore accommodate more species than can higher-latitude climates. Tropical species can become specialized on a narrow range of resources—a few food items, a specialized habitat—without a high risk of extinction [as argued for terrestrial organisms by Janzen (1967) and Ghalambor *et al.* (2006)] and thus require a smaller fraction of the diversity-dependent factors, on average, than at high latitudes. Despite such specialization, many tropical species attain broad distributions due to the relative stability of many aspects of the tropical environment (Roy *et al.*, 1994). The temperate latitudes, with levels of seasonality intermediate between tropical and polar zones, are intermediate in these features. We speculate that extinctions are

driven chiefly, though not exclusively, by changes in diversity-independent factors, such as episodes of increased environmental harshness. The amplitudes of such episodes—which may be more problematic for organisms than absolute values of environmental parameters (Compton *et al.*, 2007)—are greater in temperate zones, where extinctions have been highest during the period of our study. Extinctions lower the standing diversity below the regional accommodation level and thus raise the invasibility, which permits the engines of origination in low latitudes to export some of their products poleward, especially those lineages with high speciation rates. This gives rise to the observed out-of-the-tropics dynamic.

Whatever the precise mechanisms that damp polar diversity, our findings clearly emphasize the need to protect today's tropical marine fauna, which is the main fount of evolutionary originality for all latitudes. Human disturbances in these regions, ranging from overfishing and pollution to climate change and sea-level rise, will have a profound impact on a planetary scale.

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Abbreviations

LDG, latitudinal diversity gradient; Ma, mega annum; S/G, species to genera.

References

Addicott, W.P. (1970) Latitudinal gradients in Tertiary molluscan faunas of the Pacific coast. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 8:287–312.

Allen, A.P. and Gillooly, J.F. (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.* 9:947–954.

Allison, P.A. and Briggs, D.E.G. (1993) Paleolatitudinal sampling bias, Phanerozoic species diversity, and the end-Permian extinction. *Geology* 21:65–68.

Alroy, J. (2000) New methods for quantifying macroevolutionary patterns and processes. *Paleobiology* 26:707–733.

Alroy, J., Marshall, B., Bambach, R.K., Bezusko, K., Foote, M., Fürsich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J., Sommers, M.G., Wagner, P.J., and Webber, A. (2001) Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proc. Natl. Acad. Sci. U.S.A.* 98:6261–6266.

Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J., Hendy, A.J.W., Holland, S.M., Ivany, L.C., Kiessling, W., Kosnik, M.A., Marshall, C.R., McGowan, A.J., Miller, A.I., Olszewski, T.D., Patzkowsky, M.E., Peters, S.E., Villier, L., Wagner, P.J., Bonuso, N., Borkow, P.S., Brenneis, B., Clapham, M.E., Fall, L.M., Ferguson, C.A., Hanson, V.L., Krug, A.Z., Layou, K.M., Leckey, E.H., Nurnberg, S., Powers, C.M., Sessa, J.A., Simpson, C., Tomasovych, A., and Visaggi, C.C. (2008) Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321:97–100.

Anderson, L.L., Hu, F.S., Nelson, D.M., Petit, R.J., and Paige, K.N. (2006) Ice-age endurance: DNA evidence of a white spruce refugium in Alaska. *Proc. Natl. Acad. Sci. U.S.A.* 103:12447–12450.

Arim, M., Abades, S.R., Neill, P.E., Lima, M., and Marquet, P.A. (2006) Spread dynamics of invasive species. *Proc. Natl. Acad. Sci. U.S.A.* 103:374–378.

Arita, H.T., and Vazquez-Dominguez, E. (2008) The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. *Ecol. Lett.* 11:653–663.

Bellwood, D.R. and Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292:1532–1534.

Bellwood, D.R., Hughes, T.P., Connolly, S.R., and Tanner, J. (2005) Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol. Lett.* 8:643–651.

Beu, A.G. (2004) Marine Mollusca of oxygen isotope stages of the last 2 million years in New Zealand. Part 1: Revised generic positions and recognition of warm-water and cool-water migrants. *Journal of the Royal Society of New Zealand* 34:111–267.

Beu, A.G. (2005) Neogene fossil tonnoidean gastropods of Indonesia. *Scripta Geologica* 130:1–186.

Bhagwat, S.A. and Willis, K.J. (2008) Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *J. Biogeogr.* 35:464–482.

Bieler, R. and Mikkelsen, P.M. (2006) Bivalvia—a look at the branches. *Zool. J. Linn. Soc.* 148:223–235.

Blackburn, T.M., and Gaston, K.J. (1996) A sideways look at patterns in species richness, or why are there so few species outside the tropics? *Biodiversity Letters* 3:44–53.

Bouchet, P. (1997) Inventorying the molluscan diversity of the world: what is our rate of progress? *Veliger* 40:1–11.

Bouchet, P., Lozouet, P., Maestrati, P., and Heros, V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biol. J. Linn. Soc. Lond.* 75:421–436.

Briggs, J.C. (2007) Marine longitudinal biodiversity: causes and conservation. *Divers. Distrib.* 13:544–555.

Brubaker, L.B., Anderson, P.M., Edwards, M.E., and Lozhkin, A.V. (2005) Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *J. Biogeogr.* 32:833–848.

Bush, A.M. and Bambach, R.K. (2004) Did alpha diversity increase during the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. *J. Geol.* 112:625–642.

Bush, A.M., Markey, M.J., and Marshall, C.R. (2004) Removing bias from diversity curves: the effects of spatially organized biodiversity on sampling-standardization. *Paleobiology* 30:666–686.

Cardillo, M. (1999) Latitude and rates of diversification in birds and butterflies. *Proc. R. Soc. Lond., B, Biol. Sci.* 266:1221–1225.

Cardillo, M., Orme, C.D.L., and Owens, I.P.F. (2005) Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* 86:2278–2287.

Compton, T.J., Drent, J., Kentie, R., Pearson, G.B., van der Meer, J., and Piersma, T. (2007) Overlap in the feeding morphology of bivalves from species-rich and species-poor intertidal flats using gill: palp ratios for comparative analyses of mollusc assemblages. *Mar. Ecol. Prog. Ser.* 348:213–220.

Connolly, S.R., Bellwood, D.R., and Hughes, T.P. (2003) Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. *Ecology* 84:2178–2190.

Crame, J.A. (2000a) Intrinsic and extrinsic controls on diversification in the Bivalvia. In *Biotic Response to Global Change: The Last 145 Million Years*, edited by S.J. Culver and P.F. Rawson, Cambridge University Press, Cambridge, pp 135–148.

Crame, J.A. (2000b) Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve faunas. *Paleobiology* 26:188–214.

Crame, J.A. (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 Rosen, B.R. (2002) Cenozoic palaeogeography and the rise of modern biodiversity patterns. In *Palaeobiogeography and Biodiversity Change: the Ordovician and Mesozoic-Cenozoic Radiations*, edited by J.A. Crame and A.W. Owen, Special Publications, The Geological Society, London, pp 153–168.

Davies, R.D., Orme, C.D.L., Storch, D., Olson, V., Thomas, G.H., Ross, S.G., Bennett, P.M., Owens, I.P.F., Blackburn, T.M., and Gaston, K.J. (2007) Topography, temperature and the global distribution of bird species richness. *Proc. R. Soc. Lond., B, Biol. Sci.* 274:1189–1197.

Evans, K.L. and Gaston, K.J. (2005) Can the evolutionary-rates hypothesis explain species-energy relationships? *Funct. Ecol.* 19:899–915.

Fitzgerald, P.C. and Carlson, S.J. (2006) Examining the latitudinal diversity gradient in Paleozoic terebratulide brachiopods: should singleton data be removed? *Paleobiology* 32:367–386.

Flessa, K.W. and Jablonski, D. (1996) The geography of evolutionary turnover: a global analysis of extant bivalves. In *Evolutionary Paleobiology*, edited by D. Jablonski, D.H. Erwin, and J.H. Lipps, University of Chicago Press, Chicago, pp 376–397.

Foote, M. (2001) Evolutionary rates and the age distributions of living and extinct taxa. In *Evolutionary Patterns*, edited by J.B.C. Jackson, S. Lidgard, and M.L. McKinney, University of Chicago Press, Chicago, pp 245–294.

Foote, M. (2007) Symmetric waxing and waning of marine invertebrate genera. *Paleobiology* 33:517–529.

Gaston, K.J. (2000a) Global patterns in biodiversity. *Nature* 405:220–227.

Gaston, K.J. (2000b) Biodiversity: higher taxon richness. *Progress in Physical Geography* 24:117–127.

Gaston, K.J. and Blackburn, T.M. (1996) The tropics as a museum of biological diversity: an analysis of the New World avifauna. *Proc. R. Soc. Lond., B, Biol. Sci.* 263:63–68.

Gaylord, B. and Gaines, S.D. (2000) Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* 155:769–789.

Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Gard.* 75:1–34.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., and Wang, G. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.* 46:5–17.

Giribet, G. and Wheeler, W. (2002) On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebr. Biol.* 121:271–324.

Goldberg, E.E., Roy, K., Lande, R., and Jablonski, D. (2005) Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *Am. Nat.* 165:623–633.

Hawkins, B.A. (2001) Ecology's oldest pattern? *Trends in Ecology and Evolution* 16:470.

Hawkins, B.A. and Porter, E.E. (2003) Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Glob. Ecol. Biogeogr.* 12:475–481.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A., and Soeller, S.A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *J. Biogeogr.* 33:770–780.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A., and Soeller, S.A. (2007) Climate, niche conservatism, and the global bird diversity gradient. *Am. Nat.* Supplement 170:S16–S27.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *Am. Nat.* 163:192–211.

Holland, S.M. and Patzkowsky, M.E. (2007) Gradient ecology of a biotic invasion: biofacies of the type Cincinnatian Series (Upper Ordovician), Cincinnati, Ohio Region, USA. *Palaios* 22:392–407.

Jablonski, D. (1993) The tropics as a source of evolutionary novelty: the post-Paleozoic fossil record of marine invertebrates. *Nature* 364:142–144.

Jablonski, D. (2005a) Evolutionary innovations in the fossil record: the intersection of ecology, development, and macroevolution. *J. Exp. Zool.* 304B:504–519.

Jablonski, D. (2005b) Mass extinctions and macroevolution. *Paleobiology* 31:192–210.

Jablonski, D. and Lutz, R.A. (1983) Larval ecology of marine benthic invertebrates—paleobiological implications. *Biol. Rev. Camb. Philos. Soc.* 58:21–89.

Jablonski, D., Roy, K., and Valentine, J.W. (2000) Analyzing the latitudinal diversity gradient in marine bivalves. In *The Evolutionary Biology of the Bivalvia*, Geological Society Special Publication, edited by E.M. Harper, J.D. Taylor, and J.A. Crame, Geological Society of London, London, pp 361–365.

Jablonski, D., Roy, K., Valentine, J.W., Price, R.M., and Anderson, P.S. (2003) The impact of the Pull of the Recent on the history of bivalve diversity. *Science* 300:1133–1135.

Jablonski, D., Roy, K., and Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.

Jackson, J.B.C. and Johnson, K.G. (2001) Measuring past biodiversity. *Science* 293:2401–2404.

Jackson, S.T. and Williams, J.W. (2004) Modern analogs in Quaternary paleocology: here today, gone yesterday, gone tomorrow? *Annu. Rev. Earth Planet. Sci.* 32:495–537.

Jansson, R. and Davies, T.J. (2008) Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecol. Lett.* 11:173–183.

Janzen, D.H. (1967) Synchronization of sexual reproduction of trees within dry season in Central America. *Evolution* 21:620–637.

Kidwell, S.M. (2005) Shell composition has no net impact on large-scale evolutionary patterns in mollusks. *Science* 307:914–917.

Kindlmann, P., Schodelbauerova, I., and Dixon, A.F.G. (2007) Inverse latitudinal gradients in species diversity. In *Scaling Biodiversity*, edited by D. Storch, P.A. Marquet, and J.H. Brown, Cambridge University Press, Cambridge, pp 246–257.

Krug, A.Z. and Patzkowsky, M.E. (2007) Geographic variation in turnover and recovery from the Late Ordovician mass extinction. *Paleobiology* 33:435–454.

Krug, A.Z., Jablonski, D., and Valentine, J.W. (2007) Contrarian clade confirms the ubiquity of spatial origination patterns in the production of latitudinal diversity gradients. *Proc. Natl. Acad. Sci. U.S.A.* 104:18129–18134.

Krug, A.Z., Jablonski, D., and Valentine, J.W. (2008) Species/genus ratios reflect a global history of diversification and range expansion in marine bivalves. *Proc. R. Soc. Lond., B, Biol. Sci.* 275:1117–1123.

Laptikhovsky, V. (2006) Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology—An Evolutionary Perspective* 27:7–14.

Longhurst, A. (1998) *Ecological Geography of the Sea*, Academic Press, San Diego.

Marquet, R. (2002) The Neogene Amphineura and Bivalvia (Protobranchia and Pteriomorphia) from kallo and Doel (Oost-Vlaanderen, Belgium). *Palaeontos* 2:1–100.

Marquet, R. (2005) The Neogene Bivalvia (Heterodonta and Anomalodesmata) and Scaphopoda from Kallo and Doel (Oost-Vlaanderen, Belgium). *Palaeontos* 6:1–142.

Martin, P.R. and Tewksbury, J.J. (2008) Latitudinal variation in subspecific diversification of birds. *Evolution* 62:2775–2788.

Martin, P.R., Bonier, F., and Tewksbury, J.J. (2007) Revisiting Jablonski (1993): Cladogenesis and range expansion explain latitudinal variation in taxonomic richness. *J. Evol. Biol.* 20:930–936.

Maurer, B.A. and Nott, M.P. (1998) Geographic range fragmentation and the evolution of biological diversity. In *Biodiversity Dynamics*, edited by M.L. McKinney and J.A. Drake, Columbia University Press, New York, pp 31–50.

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.

Miller, A.I. and Foote, M. (1996) Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* 22:304–309.

Mittelbach, G.G., Schemske, D., Cornell, H.V., Allen, A.P., Brown, J.H., Bush, M., Harrison, S.P., Hurlbert, A., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M., and Turelli, M. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. *Ecol. Lett.* 10:315–331.

Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P., and Ludsin, S.A. (2003) Patterns and processes in reef fish diversity. *Nature* 421:933–936.

Mora, C., Tittensor, D.P., and Myers, R.A. (2008) The completeness of taxonomic inventories for describing the global diversity and distribution of marine fishes. *Proc. R. Soc. Lond., B, Biol. Sci.* 275:149–155.

Morley, S.A., Peck, L.S., Tan, K.S., Martin, S.M., and Portner, H.O. (2007) Slowest of the slow: latitudinal insensitivity of burrowing capacity in the bivalve *Laternula*. *Mar. Biol.* 151:1823–1830.

Novack-Gottshall, P.M., and Miller, A.I. (2003) Comparative geographic and environmental diversity dynamics of gastropods and bivalves during the Ordovician Radiation. *Paleobiology* 29:576–604.

Ozawa, T., Tanaka, T., and Tomida, S. (1998) Pliocene to Early Pleistocene warm water molluscan fauna from the Kakegawa Group, central Japan. *Nagoya University Furukawa Museum Special Report* 7:1–206.

Patzkowsky, M.E. and Holland, S.M. (1996) Extinction, invasion, and sequence stratigraphy: patterns of faunal change in the Middle and Upper Ordovician of the eastern United States. In *Special Paper 306: Paleozoic Sequence Stratigraphy; Views from the North American Craton*, Geological Society of America, Boulder, CO, pp 131–142.

Paulay, G. and Meyer, C. (2006) Dispersal and divergence across the greatest ocean barrier: do larvae matter? *Integr. Comp. Biol.* 46:269–281.

Powell, M.G. (2007) Latitudinal diversity gradients for brachiopod genera during late Palaeozoic time: links between climate, biogeography and evolutionary rates. *Glob. Ecol. Biogeogr.* 16:519–528.

Reaka, M.L., Rodgers, P.J., and Kudla, A.U. (2008) Patterns of biodiversity and endemism on Indo-West Pacific coral reefs. *Proc. Natl. Acad. Sci. U.S.A.* 105:11474–11481.

Renema, W., Bellwood, D.R., Braga, J.C., Bromfield, K., Hall, R., Johnson, K.G., Lunt, P., Meyer, C.P., McMonagle, L.B., Morley, R.J., O'Dea, A., Todd, J.A., Wesselingh, F.P., Wilson, M.E.J., and Pandolfi, J.M. (2008) Hopping hotspots: global shifts in marine biodiversity. *Science* 321:654–657.

Ricklefs, R.E. (2007) Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* 22:601–610.

Ricklefs, R.E. and Schluter, D. (1993) Species diversity: regional and historical influences. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, edited by R.E. Ricklefs and D. Schluter, University of Chicago Press, Chicago, pp 350–363.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*, Cambridge University Press, Cambridge.

Rowe, K., Heske, E., Brown, P., and Paige, K. (2004) Surviving the ice: northern refugia and postglacial colonization. *Proc. Natl. Acad. Sci. U.S.A.* 101:10355–10359.

Roy, K. and Goldberg, E.E. (2007) Origination, extinction and dispersal: integrative models for understanding present-day diversity gradients. *Am. Nat.* 170:S71–S85.

Roy, K., Jablonski, D., and Valentine, J.W. (1994) Eastern Pacific molluscan provinces and latitudinal diversity gradient—no evidence for Rapoport's Rule. *Proc. Natl. Acad. Sci. U.S.A.* 91:8871–8874.

Roy, K., Jablonski, D., and Valentine, J.W. (1995) Thermally anomalous assemblages revisited: patterns in the extraprovincial latitudinal range shifts of Pleistocene marine mollusks. *Geology* 23:1071–1074.

Roy, K., Jablonski, D., and Valentine, J.W. (2000) Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proc. R. Soc. Lond., B, Biol. Sci.* 267:293–299.

Roy, K., Jablonski, D., and Valentine, J.W. (2001) Climate change, species range limits and body size in marine bivalves. *Ecol. Lett.* 4:366–370.

Sepkoski, J.J. (2002) A compendium of fossil marine animal genera. *Bulletins of American Paleontology* 363:1–563.

Simberloff, D. (1970) Taxonomic diversity of island biotas. *Evolution* 24:23–47.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdana, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., and Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57:573–583.

Stebbins, G.L. (1974) *Flowering Plants: Evolution above the Species Level*, Harvard University Press, Cambridge, MA.

Stehli, F.G., Douglas, R.G., and Newell, N.D. (1969) Generation and maintenance of gradients in taxonomic diversity. *Science* 164:947–949.

Tomida, S. (1996) Late Neogene tropical and subtropical molluscan faunas from the South Fossa-Magna region, central Japan. *Bulletin of the Mizunami Fossil Museum* 23:89–140.

Valentine, J.W. (1968) Climatic regulation of species diversification and extinction. *Geol. Soc. Am. Bull.* 79:273–276.

Valentine, J.W. (1972) Conceptual models of ecosystem evolution. In *Models in Paleobiology*, edited by T.J.M. Schopf, Freeman, Cooper, San Francisco, pp 192–215.

Valentine, J.W. (1973) *Evolutionary Paleoecology of the Marine Biosphere*, Prentice-Hall, Englewood Cliffs, NJ.

Valentine, J.W. (1989) How good was the fossil record? Clues from the California Pleistocene. *Paleobiology* 15:83–94.

Valentine, J.W. and Jablonski, D. (1993) Fossil communities: compositional variation at many time scales. In *Species Diversity in Ecological Communities*, edited by R.E. Ricklefs and D. Schluter, University of Chicago Press, Chicago, pp 341–349.

Valentine, J.W., Jablonski, D., Kidwell, S., and Roy, K. (2006) Assessing the fidelity of the fossil record by using marine bivalves. *Proc. Natl. Acad. Sci. U.S.A.* 103:6599–6604.

Valentine, J.W., Jablonski, D., Krug, A.Z., and Roy, K. (2008) Incumbency, diversity, and latitudinal gradients. *Paleobiology* 34:169–178.

Vermeij, G.J. (2001) Community assembly in the sea: geological history of the living shore biota. In *Marine Community Ecology*, edited by M.D. Bertness, S.D. Gaines, and M.E. Hay, Sinauer Associates, Inc., Sunderland, MA, pp 39–60.

Weir, J.T. and Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315:1574–1576.

Wiens, J.J. (2007) Global patterns of diversification and species richness in amphibians. *Am. Nat.*, Supplement 170:S86–S106.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A., and Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *Am. Nat.* 168:579–596.

Williams, S.T. (2007) Origins and diversification of Indo-West Pacific marine fauna: evolutionary history and biogeography of turban shells (Gastropoda, Turbinidae). *Biol. J. Linn. Soc. Lond.* 92:573–592.

Williams, S.T. and Duda, T.F. (2008) Did tectonic activity stimulate Oligo-Miocene speciation in the Indo-West Pacific? *Evolution* 62:1618–1634.

Willig, M.R., Kaufman, D.M., and Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* 34:273–309.

Wood, S.V. (1874) *A Monograph of the Crag Mollusca or Descriptions of Shells from the Middle and Upper Tertiaries of the East of England. Vol. III. Univalves and Bivalves*, Palaeontographical Society, London.

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