Paleobiology, 41(2), 2015, pp. 330–341
DOI: 10.1017/pab.2014.20

Origination, extinction, invasion, and extirpation components of the brachiopod latitudinal biodiversity gradient through the Phanerozoic Eon

Matthew G. Powell, Brandi R. Moore, and Travis J. Smith

Abstract.—The geographic distribution of brachiopod genus occurrences over the Phanerozoic shows that secular declines in origination and extinction rates were paralleled by increases in invasion and extirpation rates. Origination and extinction rates declined in two phases, the first from the Cambrian to latest Permian Periods and the second from the latest Permian Period to the present, which were accompanied by concomitant increases in invasion and extirpation rates. In addition to the temporal correlation, an inverse correlation was also weakly evident among time-averaged latitudinal gradients of rates. Compared with faunas at higher latitudes, low-latitude faunas experienced higher origination and extinction rates, and lower invasion and extirpation rates. We suggest that progressive increases in migration ability lowered origination and extinction rates because species that were better equipped to track a preferred habitat, for example, by the ability to disperse larvae over large distances, were less likely to evolve or become extinct in response to local environmental changes. The two phases were separated by the end-Permian mass extinction, which reset to high levels the origination and extinction rates of a taxonomically and ecologically altered global brachiopod fauna. Our data also allow us to quantify the relative contributions of origination, extinction, invasion, and extirpation to regional diversity (quantified as 10° latitudinal zones) more generally. Overall, invasion and extirpation explained slightly more variation in diversity than in situ origination and extinction. The four variables usually occurred in combinations that maintained rather than altered the shape of the latitudinal diversity gradient. For most of the Phanerozoic Eon, the gradient was not the product of continuous renewal, but rather existed as a holdover from a previous interval.

Matthew G. Powell, Brandi R. Moore, and Travis J. Smith. Department of Geology, Juniata College, 1700 Moore Street, Huntingdon, Pennsylvania 16652, U.S.A. E-mail: powell@juniata.edu

Accepted: 15 October 2014

Supplemental materials deposited at Dryad: doi:10.5061/dryad.7k7k5

Introduction

Secular trends of global biodiversity have been studied for several decades (e.g., Newell 1959; Sepkoski 1978, 1979, 1984, 1988, 1993; Sepkoski et al. 1981; Raup and Sepkoski 1982; Labandeira and Sepkoski 1993; Alroy et al. 2001, 2008). In contrast, only recently has it become possible to adequately quantify spatial variation in biodiversity over geologic time. The preeminent geographic pattern is the latitudinal biodiversity gradient (LBG), which is nearly ubiquitous across taxa (Hillebrand 2004; Mittelbach et al. 2007) and through time (Crame 2001; Powell 2009; Naimark and Markov 2011). One of its fundamental characteristics is the latitude at which peak biodiversity occurs. Present-day marine biodiversity generally reaches its maximum at around 10–20°N (Valentine et al. 2009; Tittensor et al. 2010; Powell et al. 2012) and declines toward both poles. In contrast, studies of fossil LBGs have documented that peak biodiversity has occurred at different latitudes over time (e.g., Renema et al. 2008; Powell 2009; Mannion et al. 2012; Yasuhara et al. 2012). Until recently, peak biodiversity of marine taxa was located around 30–40°N (Powell 2009; Naimark and Markov 2011); it appears to have shifted toward the equator in the last few tens of millions of years for some taxa (Renema et al. 2008) but not others (Powell 2009). These findings challenge the implicit assumptions that peak diversity occurs at the equator (as when diversity is regressed on latitude) and that the source of evolutionary novelty is some factor(s) intrinsic to the tropical environment. Our ability to reconcile these patterns and reach a full understanding of the dynamics of the LBG over time requires accurate reconstructions not only of

0094-8373/15

the LBG, but also of its proximal controls. Here, we report Phanerozoic-scale, latitudinal gradients of macroevolutionary rates (origination and extinction) and geographic range shifts (invasion and extirpation) for a monophyletic, well-preserved, and taxonomically well-described taxon, the Brachiopoda, using sample-standardized occurrence data from the Paleobiology Database (http://paleodb.org).

Diversity within a region changes as the result of four factors: the rates at which taxa originate or invade a region, and the rates at which taxa become extinct or are extirpated from a region (Hawkins and Porter 2003; Jablonski et al. 2006; Mittelbach et al. 2007; Roy and Goldberg 2007). We refer to these four components as the proximal controls of diversity in order to distinguish them from the ultimate processes that control speciation, extinction, and geographic range shifts (e.g., Stanley 1990). Total diversity within a region also depends on the number of holdover taxa (survivors) from the previous interval. Many studies of the proximal controls of the present-day LBG have focused on whether the tropics are a "cradle" or "museum" of diversity (Jablonski 1993; Chown and Gaston 2000; Goldberg et al. 2005; Mittelbach et al. 2007; Arita and Vázquez-Domínguez 2008), that is, whether diversity is high in the tropics because of high origination rates (=cradle) or because of low extinction rates (=museum). The available empirical evidence suggests that both speciation and extinction rates tend to be highest at low latitudes (Stehli et al. 1969; Stehli and Wells 1971; Rohde 1992; Jablonski 1993; Flessa and Jablonski 1996; Crame 1997; Crame and Rosen 2002; Martin and McKay 2004; Powell 2007; Krug et al. 2009). High tropical diversity is apparently due to high speciation rates that outpaced high extinction rates (Crame 2000; Buzas et al. 2002). High tropical origination and extinction rates have been linked to the large proportion of endemic taxa in that region (Stanley and Powell 2003; Powell 2005, 2007), which tend to have intrinsically higher speciation and extinction rates (Stanley 1990).

The role of geographic range shifts (by invasion or extirpation) has received less attention than in situ speciation and extinction rates (Roy and Goldberg 2007). The most comprehensive analysis of a link between macroevolution and geographic range shifts is the "out of the tropics" model (Jablonski et al. 2006; Krug et al. 2007; Valentine et al. 2009; Jablonski et al. 2013), which proposes that the tropics serve as a diversity pump as species originate at low latitudes and then invade higher latitudes. Because of the rapidity with which species can alter their ranges (Root et al. 2003; Parmesan 2006), it is difficult to capture geographic range changes with fossil data, and so this "out of the tropics" model has been formulated and tested mainly with living taxa. There are some indications that the "out of the tropics" model is strictly true only for the present-day fauna, and that the mechanism by which taxa originate in a particular area and then spread to higher latitudes is not necessarily localized to the tropics but occurs wherever the center of origin of a particular taxon may be. For example, Krug et al. (2007) demonstrated that high speciation rates co-occurred with the area of highest diversity in the Anomalodesmata, a clade of bivalves that have a reverse LBG. Likewise, Beadle (1991) documented an "into the tropics" spread of dendrasterid sand dollars after they originated at northern midlatitudes during the late Miocene.

Our compilation of secular latitudinal trends of the four proximal controls of biodiversity demonstrates a previously undescribed inverse relationship between macroevolutionary rates and geographic range shifts, which generally acted together to maintain an LBG over time. More generally, this study is the first to document secular latitudinal trends of macroevolutionary rates and geographic range shifts that underlie the LBG, and therefore provides the most comprehensive understanding yet of how these factors varied to produce observed diversity.

Methods

We downloaded 130,777 fossil occurrences for 3166 brachiopod genera from the Paleobiology Database, spanning the past 536 Myr (downloaded on 18 December 2012; search parameters, raw data, references, and contributors are available as supplementary online information). We refined the data set by removing genera represented by a single occurrence ($n = 529$), and all occurrences dated less precisely than 20 Myr ($n = 5311$), resulting in a final data set consisting of 124,937 occurrences for 2632 genera. Single-occurrence genera are unsuitable for geographic analyses because it is extremely difficult to determine whether a taxon was truly geographically restricted, or widespread but undetected (Buzas et al. 1982).

These occurrences were grouped into bins 10 Myr long by 10° latitude wide, which provided an acceptable resolution for analyzing broad-scale patterns while maintaining sufficient within-bin sample sizes. The quality of our data set is affected by several factors. First, occurrences may be assigned to an incorrect time bin if they were dated incorrectly by the original author, or if the midpoint age was insufficiently precise. Second, diversity changes across intervals may be dampened because boundaries between the 10-Myr time intervals chosen for this study do not necessarily coincide with important paleontological boundaries. For example, the 450–440 Ma bin lumps the end-Ordovician mass extinction (ca. 444 Ma) with early Silurian rediversification, diminishing the apparent magnitude of this major event. Third, to calculate results, we used only taxa actually sampled within each bin, rather than counting overlapping polygons encompassing known occurrences. The overlapping polygon method, used in previous studies (Powell 2007, 2009), compensates for undersampling by projecting occupancy into bins in which a taxon was not necessarily sampled but was likely to have occurred. Using a sampled-in-bin method introduces more volatility to the results, but allows diversity estimates to be standardized by the number of occurrences, thus increasing confidence in estimates calculated for bins in which taxa are actually found. For these reasons, our data should be interpreted as reflecting broad-scale trends rather than true interval-by-interval variation.

We then used the occurrences to quantify diversity, origination, extinction, invasion, and extirpation within each bin (Fig. 1), using Fisher's alpha (α) to correct for variation in sampling effort (Fisher et al. 1943; Hayek and Buzas 1997). Fisher's α is a commonly used biodiversity metric that is calculated recursively from two measured variables, the number of occurrences (N) and the number of taxa (S), using the equation $S = \alpha \bullet \ln[1 + (N/\alpha)]$. Fisher's α is independent of sample size provided that the data conform to a log-series distribution (Hayek and Buzas 1997; Magurran 2004), which is true for our data ($r^2 = 0.98$, $p < 0.001$). Unlike several other sample-standardization methods, α does not assume that variation in the number of occurrences is necessarily due to differences in sampling effort (Hayek and Buzas 1997), a property it shares with a relatively new metric, shareholder quorum subsampling (SQS; Alroy 2010). For our data, α and SQS diversity are highly correlated (see below) and the results would be essentially identical had we used SQS. Certain combinations of N and S result in values of α that are not biologically meaningful because the value of α is greater than the number of sampled genera (Hayek and Buzas 1997). In these cases, we replaced α with S, and replaced rates that were greater than one with a rate of one, because more than 100% of taxa cannot have arrived (by origination or invasion) or departed (by extinction or extirpation) from a bin. The sum of rates within a bin may be more than one, because a genus may count in more than one category; e.g., a genus may have invaded a latitudinal bin before becoming extinct during the same time interval. These substitutions affected 20% of diversity bins (96 of 485 bins with non-zero diversity), 2.7% of extinction bins (13 of 485), 3.9% of origination bins (19 of 485), 7.6% of extirpation bins (37 of 485), and 8.6% of invasion bins (42 of 485).

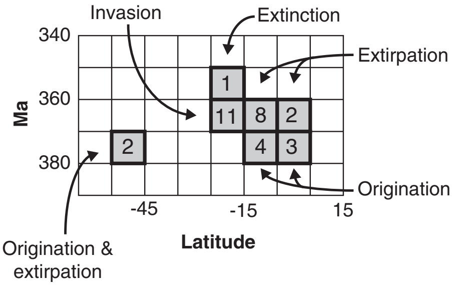

FIGURE 1. Method used to enumerate origination, extinction, invasion, and extirpation, using occurrence data for *Leioproductus* as an example. The number of *Leioproductus* occurrences is given in each occupied (shaded) bin.

Global diversity calculated as α closely resembles secular patterns of diversity generated by other methods. Fisher's α is highly correlated with (1) range-through diversity calculated from the Sepkoski et al. (2002) data set after interpolation to 10-Myr bins (accessed from http://strata.geology.wisc.edu/jack/; $r = 0.75$, $p < 0.0001$), (2) sampled diversity in 10-Myr bins obtained from the Paleobiology Database ($r = 0.79$, $p < 0.0001$), and (3) diversity data from the Paleobiology Database after sample-standardization by SQS ($r = 0.77$, $p < 0.0001$).

Results

Geography of Origination, Extinction, Invasion, and Extirpation.—Sample-standardized rates of origination, extinction, invasion, and extirpation are presented in Figure 2. Averaged across all bins, mean invasion and extirpation rates were significantly greater than mean origination and extinction rates (Fig. 3). We assessed the relative importance of each factor to changes in diversity by regressing the Fisher's α of originations, extinctions (in the previous interval), invasions, and extirpations (in the previous interval) on the change in diversity from the previous interval, after removing bins with zero diversity ($n = 560$, $r^2 = 0.85$, $p < 0.0001$). All four factors contributed significantly to changes in diversity (Table 1). However, the standardized coefficients for invasion and extirpation were greater than those of origination and extinction by a factor of about 1.3; i.e., changes in regional diversity are determined more by existing taxa invading or becoming extirpated from a region than by in situ origination or extinction. Survival rates were comparable to origination and extinction rates (Fig. 3), indicating that, at this geographic and temporal scale, holdover taxa contribute substantially to total diversity within a region.

Major mass extinctions and radiations were not necessarily latitudinally extensive (Fig. 2). Geographically prominent extinction events occurred during the last interval of the Permian Period (260–250 Ma) and the last interval of the Triassic Period (210–200 Ma). During the late Permian event, extinction rates exceeded 80% over at least three-quarters of the globe (13 of 17 latitudinal bins), and during the Triassic event, they exceeded 60% over nearly half of the globe (8 of 17 latitudinal bins). Geographically prominent origination events occurred during the Early Cambrian Period (530–520 Ma) and the first interval of the Triassic Period (250–240 Ma). Brachiopods simultaneously appeared in 10 of 17 latitudinal bins within a 10-Myr interval of the Early Cambrian. During the earliest Triassic, origination rates exceeded 60% over more than half the globe (9 of 17 latitudinal bins) as the brachiopod fauna recovered from the end-Permian event. Other major events were not as geographically extensive. For example, mass extinctions at the end-Ordovician (450–440 Ma), Late Devonian, and end-Jurassic (160–150 Ma) were taxonomically severe for brachiopods, but were restricted to a narrow latitudinal zone. In general, these major origination and extinction events were not accompanied by unusual patterns of invasion or extirpation (Fig. 2); i.e., they did not involve major shifts in geographic distribution.

Broad-scale trends in origination and extinction rates, once averaged across time and latitude, were inversely related to invasion and extirpation rates. Zonally averaged origination and extinction rates declined in two phases, the first from Cambrian to late Permian time, and the second from latest Permian time to the present. These declines were paralleled by concomitant increases in zonally averaged invasion and extirpation rates (Fig. 4). Average geographic range size, quantified as the mean number of occupied latitudinal bins (Fig. 5), did not trend significantly during the first interval ($r^2 = 0.02$, $p = 0.4$), but declined from the latest Permian to the present ($r^2 = 0.5$, $p < 0.0001$; results were the same when geographic range was quantified as the total latitudinal range rather than number of occupied bins; Cambrian–late Permian: $r^2 = 0.002$, $p = 0.8$, latest Permian–present: $r^2 = 0.3$, $p = 0.002$).

Time-averaged latitudinal gradients showed a weaker, but similar, inverse relationship between macroevolutionary rates and geographic range shifts. Mean rates of origination and extinction, averaged across time bins, tended to be highest at low latitudes, whereas mean rates of invasion and extirpation tended

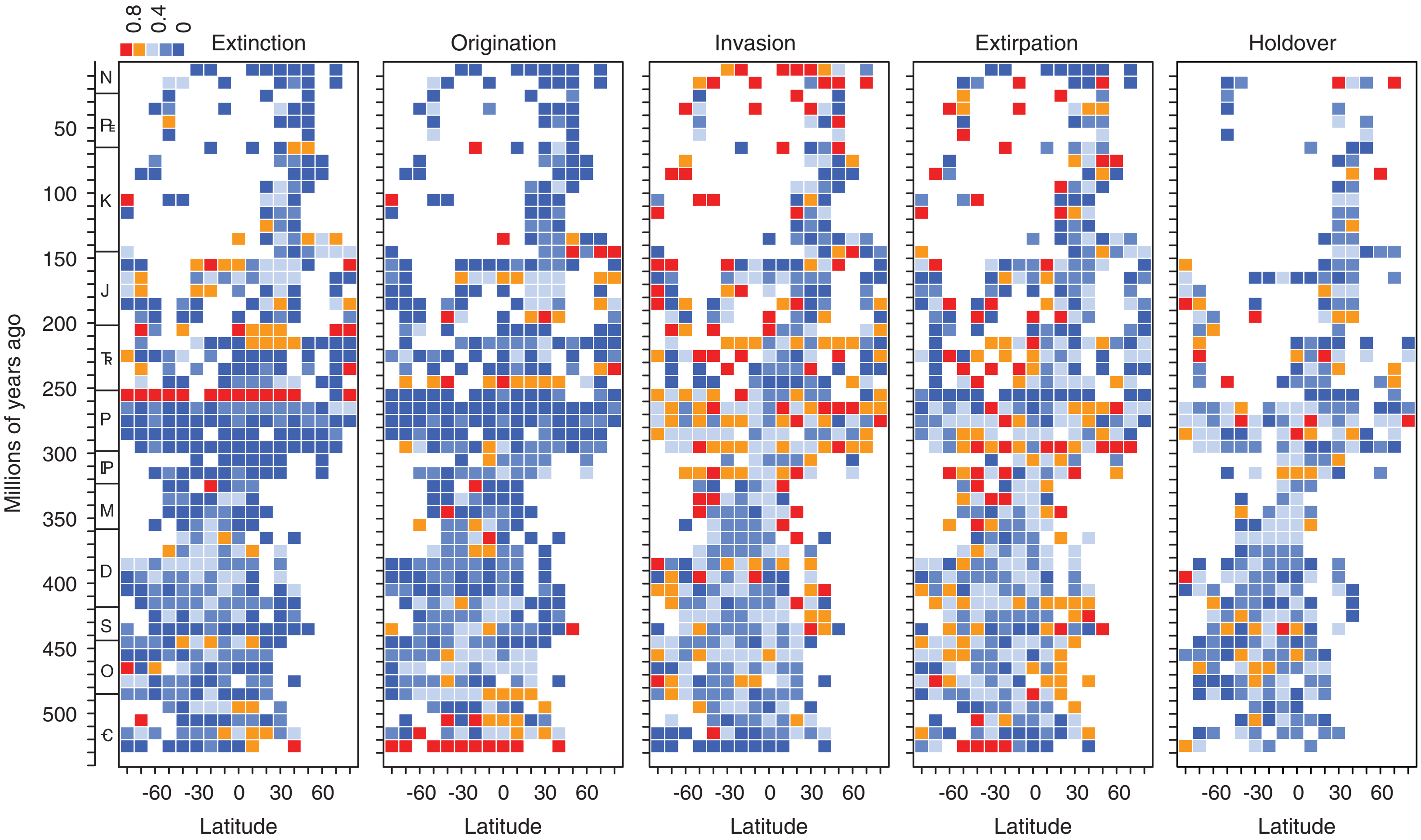

FIGURE 2. Sample-standardized geographic patterns of extinction, origination, invasion, extirpation, and survival (holdover) rates, in 10-Myr × 10° latitude bins. Rates were calculated by determining Fisher's α of genera in each category and then dividing by Fisher's α of the total number of genera in the bin. For example, if a bin contained 100 occurrences of 20 genera, and 5 of the genera represented by 25 of the occurrences became extinct in that bin, the extinction rate is $\alpha_{[25,\ 5]} / \alpha_{[100,\ 20]} = 1.9/7.5 = 0.25$. Sample-standardized rates were highly correlated with nonstandardized rates (all pairwise comparisons $r > 0.83$, $p < 0.001$). Holdover taxa do not contribute to changes in diversity, but are included here because they partially determine total diversity in a region.

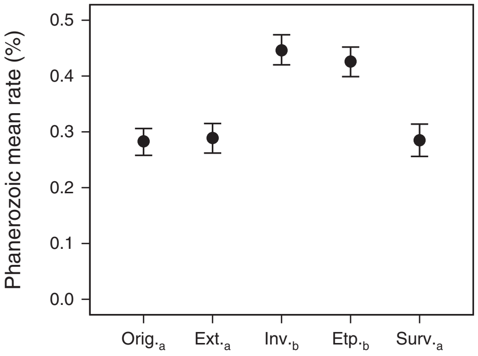

FIGURE 3. Phanerozoic mean rates and bootstrapped 95% confidence intervals of origination (Org.), extinction (Ext.), invasion (Inv.), extirpation (Etp.), and survival (Surv.). The rates significantly differed from one another, $p < 0.0001$. Means with the same subscript were not significantly different at the 0.05 significance level using Fisher's Least Significant Difference test.

TABLE 1. Standardized coefficients (β) from a multiple regression of four predictors on change in diversity. Standardized coefficients assess the degree to which changes in the predictor change the dependent variable. Variance inflation factors were all less than 10 (origination = 1.5, immigration = 1.6, extinction = 1.3, emigration = 1.3), indicating that multicollinearity did not affect the statistical significance of the individual predictors (O'Brien 2007).

	β	p
Origination$_t$	0.33	<0.0001
Extinction$_{t-1}$	−0.41	<0.0001
Invasion$_t$	0.53	<0.0001
Extirpation$_{t-1}$	−0.53	<0.0001

to be lowest at low latitudes (Fig. 6). These trends were evident only in the data between 60°S and 60°N, and the trend was evident but not statistically significant for invasion and extirpation rates.

Geography of Diversity.—The general volatility of origination, extinction, invasion, and extirpation rates contrasts with the relative stability of diversity over time (Fig. 7). The sample-standardized pattern of diversity compiled here shows the same basic pattern as an earlier study of brachiopods compiled from a different data set (Powell 2009), and with results for all marine invertebrates compiled from the Paleobiology Database (Naimark and Markov 2011). Our new data permit a slightly more refined understanding of brachiopod diversity over time: the latitudinal distribution of diversity shows three distinct phases occurring at different times of the Phanerozoic, each characterized by a different shape of the mean LBG (Fig. 8). The first interval covered the Paleozoic Era, during which brachiopods were generally present everywhere there was continental shelf area, which included all but high northern latitudes until Pangea formed during the Pennsylvanian Period. The second interval covered the Triassic through Jurassic Periods, during which brachiopods maintained broad latitudinal coverage but were most diverse in the northern midlatitudes. The third interval covered the Cretaceous Period to the present. During this interval, diversity was bimodally distributed as the northern midlatitude peak persisted from the second interval and a southern mid-latitude peak developed in the middle Cretaceous Period, while becoming scarce elsewhere, particularly in the tropics. A few genera repopulated the tropics toward the end of this third interval (approximately the middle Eocene; Fig. 7).

In most cases, the combination of origination, extinction, invasion, and extirpation was not sufficient to reestablish a new LBG in any one time interval. We tested whether the change in diversity from the previous interval was distributed uniformly among latitudinal bins, using a Kolmogorov-Smirnov exact test. Even at a very liberal significance level of $\alpha = 0.05$ (uncorrected for multiple comparisons), changes in diversity were distributed non-uniformly in only eight of the 53 10-Myr time intervals. These intervals included the early Cambrian (530–520 Ma, $p = 0.02$), late Cambrian–early Ordovician (490–480 Ma, $p = 0.01$), late Permian (280–270 Ma, $p = 0.003$; 270–260 Ma, $p = 0.003$; 260–250 Ma, $p = 0.01$), middle Triassic (240–230 Ma, $p = 0.002$; 230–220 Ma, $p = 0.03$), and early Jurassic (190–180 Ma, $p = 0.02$). In most intervals, the existence of an LBG was not the result of geologically recent processes that created or enhanced an uneven latitudinal distribution of diversity, but was instead a holdover from a previous interval.

Discussion

The Phanerozoic decline in origination and extinction rates seen in our brachiopod data was first documented for the global marine

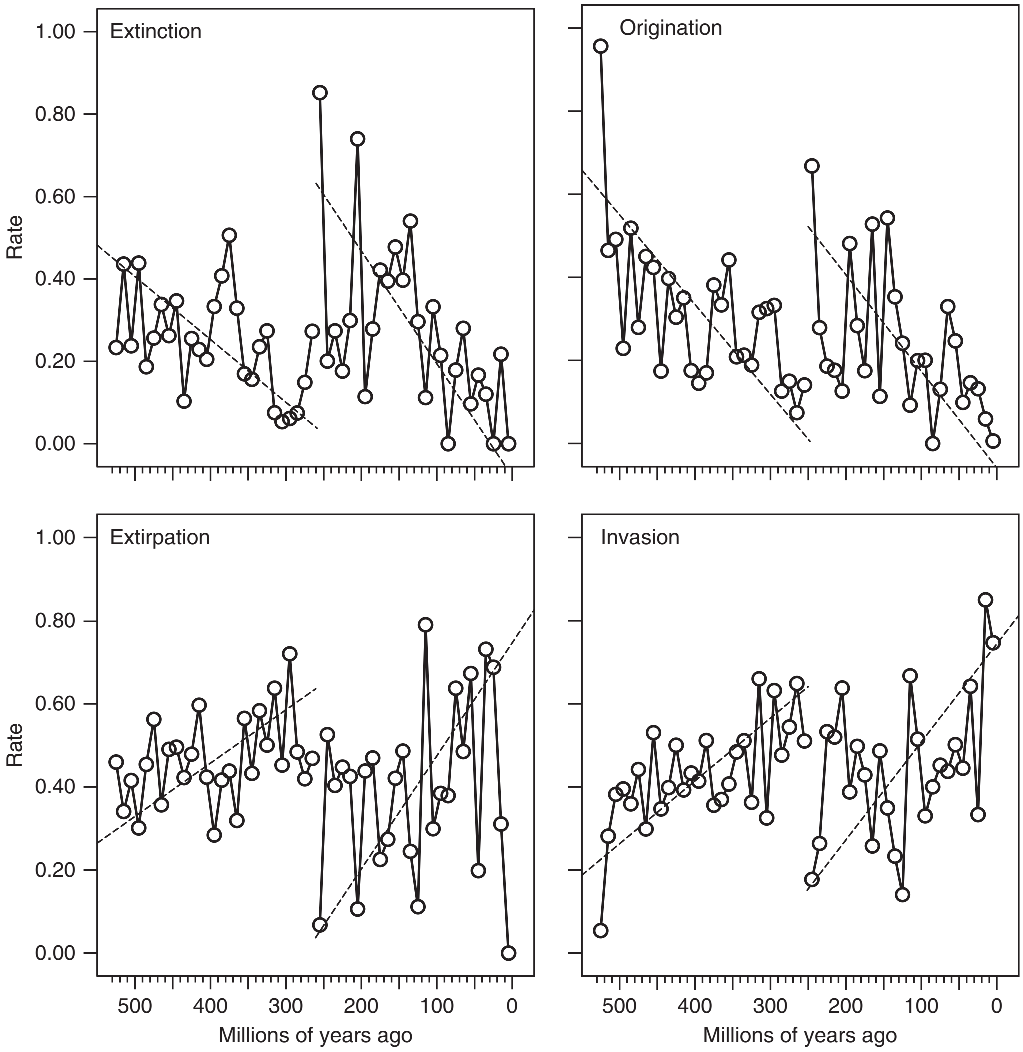

FIGURE 4. Zonally averaged rates of origination, extinction, invasion, and extirpation over time. Trend (dashed) lines were fit by reduced major axis regression.

fauna by Raup and Sepkoski (1982). Gilinsky (1994) explained the decline as the progressive culling of higher taxa with intrinsically high origination and extinction rates. These taxa were eliminated because their diversity histories were more volatile and therefore more likely to be completely eliminated. Unlike the decline described by Raup and Sepkoski (1982), however, the brachiopod decline seen here is best modeled as two declines that were separated by the end-Permian mass extinction, which reset origination and extinction rates to high levels. Non-monotonic declines in extinction rate have been described by Van Valen (1984; a two-phase decline separated by the end-Permian mass extinction) and Bambach et al. (2004; a three-phase decline separated by the end-Ordovician and end-Permian mass extinctions). The two-phase pattern exhibited by brachiopods may be explained by the fact that the Paleozoic and post-Paleozoic brachiopod faunas were almost entirely taxonomically distinct, owing to the severity of the end-Permian mass extinction (just 1.4% of all genera are present in both intervals). Following the end-Permian event, the culling process described by Gilinsky (1994) acted anew on an ecologically similar but essentially evolutionarily distinct fauna. A two-phase decline may not be as evident in the entire marine fauna (Raup and Sepkoski 1982) because many of the component taxa did not suffer in the end-Permian event as severely as the brachiopods.

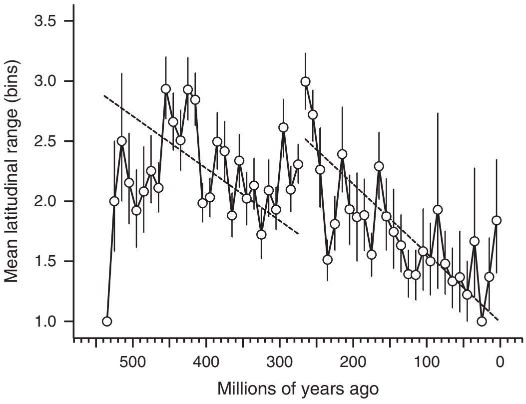

FIGURE 5. Mean number of occupied latitudinal bins per time interval with bootstrapped 95% confidence intervals. Trend (dashed) lines were fit by reduced major axis regression.

Our results suggest that long-term changes in origination and extinction rates were closely related to the ability of brachiopods to shift their geographic ranges. The connection between macroevolutionary rates and geographic range shifts was first made by Stanley (1990), who suggested that taxa with greater dispersal ability have lower origination rates because dispersal limits the formation of isolated populations. These taxa also have lower extinction rates because dispersal produces a widespread, stable population resistant to disturbance. The benefits of a widespread geographic range are well known (Jablonski 2005; Payne and Finnegan 2007): the larger the geographic range, the more widespread a perturbation has to be to completely eliminate the population. However, this reasoning

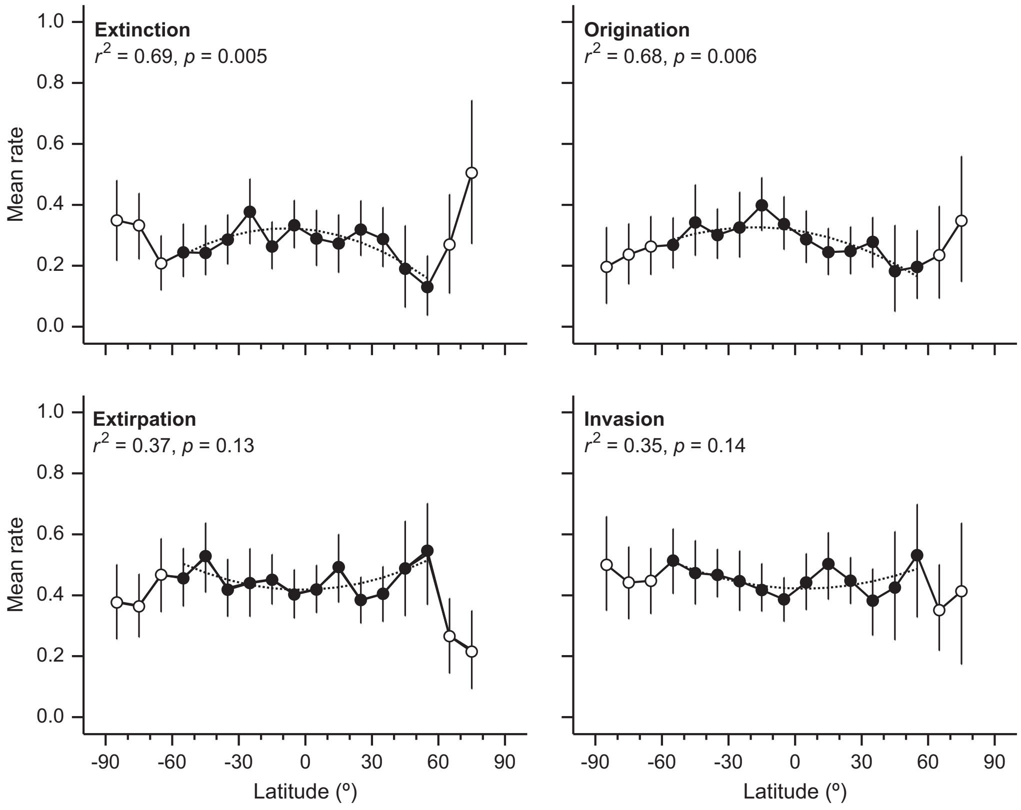

FIGURE 6. Time-averaged rates and bootstrapped 95% confidence intervals of origination, extinction, invasion, and extirpation.

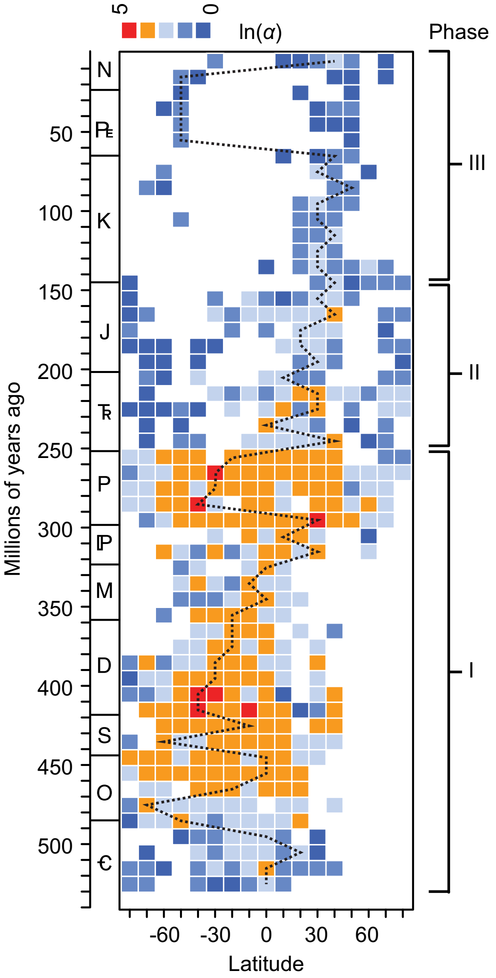

FIGURE 7. Sample-standardized geographic pattern of diversity during the Phanerozoic Eon, in 10-Myr × 10° latitude bins. Note that a log scale is used for Fisher's α so that fine detail is not obscured by binning. Dotted line indicates the latitudinal position of peak biodiversity.

cannot explain the long-term declines in origination and extinction observed here, because the average latitudinal range of brachiopods trended nonsignificantly during the first phase and decreased during the second, the opposite of the expected relationship. The fact that invasion and extirpation rates increased over this time interval suggests instead that greater dispersal ability conferred extinction resistance because it enabled species to escape selection pressures by tracking favored environments. Over time, taxa with poor dispersal ability, and hence intrinsically high origination and extinction rates, were replaced by taxa able to

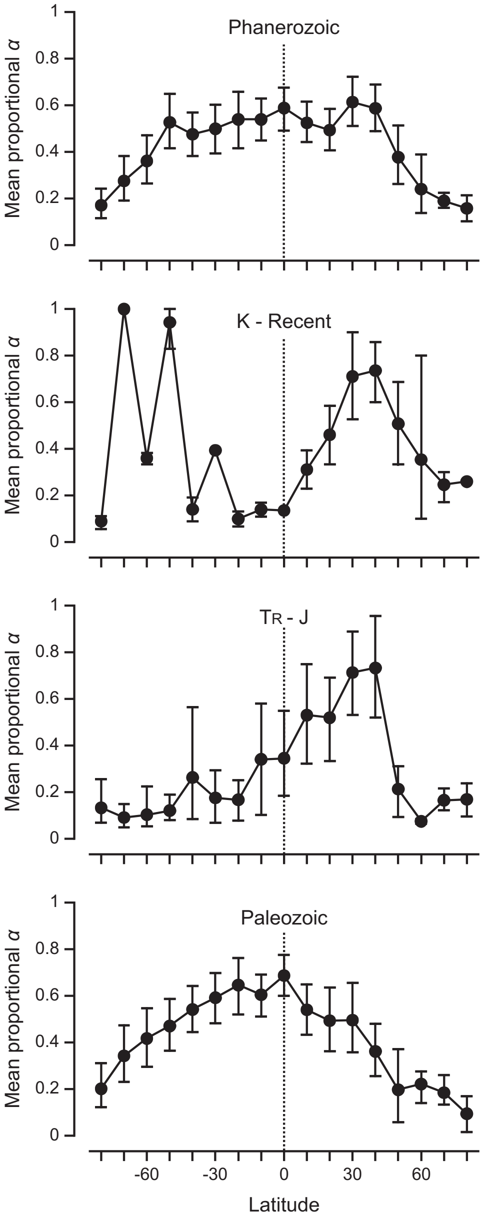

FIGURE 8. Average latitudinal biodiversity gradients (mean normalized Fisher's α and bootstrapped 95% confidence intervals) for the Phanerozoic Eon, Paleozoic Era, Triassic–Jurassic Periods, and Cretaceous Period to present. Diversity within each bin was normalized by dividing by the maximum diversity in that interval before averaging, so that the average shape was not distorted by differences in the absolute magnitude of diversity between intervals.

withstand environmental change by shifting their geographic range, thus buffering them from extinction while reducing the probability of allopatric speciation. This same negative relationship was also weakly evident as a latitudinal trend. Tropical regions harbor high biodiversity today because they contain many endemic taxa (Myers et al. 2000; Roberts et al. 2002), which, by definition, have small geographic range sizes and therefore intrinsically high origination and extinction rates (Stanley 1990). Conversely, higher latitudes generally contain taxa that are broadly adapted, because environmental conditions there vary considerably on both ecological and geological time scales (Addo-Bediako et al. 2000). Consequently, taxa living at higher latitudes typically have large geographic range sizes and a greater ability to shift their geographic ranges in response to changing environmental conditions, and, therefore, exhibit intrinsically low rates of origination and extinction. This hypothesis cannot be tested directly because adequate data on secular or latitudinal trends in the dispersal ability of brachiopods have not been reported in the literature. In living brachiopods, higher fecundity is associated with larger body sizes (Williams et al. 1997), which increased through the Paleozoic (Novack-Gottshall and Lanier 2008). This trend may underlie the secular pattern documented here, if higher fecundity increased the probability of dispersing widely.

Overall, the fact that regional diversity was determined more by invasion and extirpation than in situ origination and extinction is not surprising. Species are able to rapidly invade new areas by shifting the boundaries of their geographic range (Root et al. 2003). By comparison, usual rates of evolution are too slow to keep up with environmental change unless phenotypic plasticity is high (Visser 2008; Quintero and Wiens 2013). As a consequence, most regions acquire more of their diversity from immigrants than in situ speciation. An illustrative example is the Hawaiian islands, which, as geographically isolated oceanic islands, contain what is considered to be a highly endemic marine fauna (Kier et al. 2009). Even so, only about one-third of the marine species are endemic (Kay and Palumbi 1987), the rest consisting of colonizers from elsewhere in the Indo-West Pacific.

In general, origination, extinction, invasion, and extirpation rates in combination tended to maintain, rather than alter, the shape of the LBG. In most intervals, the LBG exists as a holdover from a previous interval rather than the result of a continuous process of renewal. Intervals for which a different shape of the LBG could arise as a result of processes occurring within one 10-Myr time interval occur over about 15% of the Phanerozoic Eon, at most. Although our results do not contradict any of the existing models to explain the LBG, they do suggest that the evolutionary dynamics characterizing any particular time interval may not be representative of other times. Living brachiopods are most diverse at midlatitudes, unlike many other marine invertebrates (Powell 2009; Tittensor et al. 2010; Powell et al. 2012), a latitudinal distribution that has remained essentially unchanged since the Jurassic. Because this study is the first to document the proximal controls of the LBG over the Phanerozoic, it is currently unclear whether the patterns documented here are similar to the underlying processes that govern the LBGs of other taxa.

Acknowledgments

This work was supported by a grant to M.G.P. from the NASA Astrobiology Program. This is Paleobiology Database publication number 214.

Literature Cited

Addo-Bediako, A., S. L. Chown, and K. J. Gaston. 2000. Thermal tolerance, climatic variability and latitude. Proceedings of the Royal Society of London B 267:739–745.

Alroy, J. 2010. Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. Quantitative methods in paleobiology. Paleontological Society Papers 16: 55–80.

Alroy, J., C. Marshall, R. Bambach, K. Bezusko, M. Foote, F. Fürsich, T. Hansen, S. Holland, L. Ivany, and D. Jablonski. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. Proceedings of the National Academy of Sciences USA 98:6261–6266.

Alroy, J., M. Aberhan, D. J. Bottjer, M. Foote, F. T. Fürsich, P. J. Harries, A. J. Hendy, S. M. Holland, L. C. Ivany, and W. Kiessling. 2008. Phanerozoic trends in the global diversity of marine invertebrates. Science 321:97–100.

Arita, H. T., and E. Vázquez-Domínguez. 2008. The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. Ecology Letters 11:653–663.

Bambach, R. K., A. H. Knoll, and S. C. Wang. 2004. Origination, extinction, and mass depletions of marine diversity. Paleobiology 30:522–542.

Beadle, S. C. 1991. The biogeography of origin and radiation: dendrasterid sand dollars in the northeastern Pacific. Paleobiology 17:325–339.

Buzas, M. A., C. F. Koch, S. J. Culver, and N. F. Sohl. 1982. On the distribution of species occurrence. Paleobiology 8: 143–150.

Buzas, M. A., L. S. Collins, and S. J. Culver. 2002. Latitudinal difference in biodiversity caused by higher tropical rate of increase. Proceedings of the National Academy of Sciences USA 99:7841–7843.

Chown, S. L., and K. J. Gaston. 2000. Areas, cradles and museums: the latitudinal gradient in species richness. Trends in Ecology and Evolution 15:311–315.

Crame, J. A. 1997. An evolutionary framework for the polar regions. Journal of Biogeography 24:1–9.

——. 2000. The nature and origin of taxonomic diversity gradients in marine bivalves. *In* E. M. Harper, J. D. Taylor, and J. A. Crame, eds. The evolutionary biology of the Bivalvia. Geological Society of London Special Publication 177:347–360.

——. 2001. Taxonomic diversity gradients through geological time. Diversity and Distributions 7:175–189.

Crame, J. A., and B. Rosen. 2002. Cenozoic palaeogeography and the rise of modern biodiversity patterns. *In* J. A. Crame and A. W. Owen, eds. Palaeobiogeography and biodiversity change: the Ordovician and Mesozoic-Cenozoic radiations. Geological Society of London Special Publication 194:153–168.

Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12:42–58.

Flessa, K. W., and D. Jablonski. 1996. The geography of evolutionary turnover: a global analysis of extant bivalves. Pp. 376–397 *in* J. W. Valentine, D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. Evolutionary paleobiology. University of Chicago Press, Chicago.

Gilinsky, N. L. 1994. Volatility and the Phanerozoic decline of background extinction intensity. Paleobiology 20:445–458.

Goldberg, E. E., K. Roy, R. Lande, and D. Jablonski. 2005. Diversity, endemism, and age distributions in macroevolutionary sources and sinks. American Naturalist 165:623–633.

Hawkins, B. A., and E. E. Porter. 2003. Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. Global Ecology and Biogeography 12:475–481.

Hayek, L., and M. A. Buzas. 1997. Surveying Natural Populations. Columbia University Press, New York.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. American Naturalist 163:192–211.

Jablonski, D. 1993. The tropics as a source of evolutionary novelty through geological time. Nature 364:142–144.

——. 2005. Mass extinctions and macroevolution. Paleobiology 31:192–210.

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

Jablonski, D., C. L. Belanger, S. K. Berke, S. Huang, A. Z. Krug, K. Roy, A. Tomašových, and J. W. Valentine. 2013. Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. Proceedings of the National Academy of Sciences USA 110:10487–10494.

Kay, E. A., and S. R. Palumbi. 1987. Endemism and evolution in Hawaiian marine invertebrates. Trends in Ecology and Evolution 2:183–186.

Kier, G., H. Kreft, T. M. Lee, W. Jetz, P. L. Ibisch, C. Nowicki, J. Mutke, and W. Barthlott. 2009. A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences USA 106:9322–9327.

Krug, A. Z., D. Jablonski, and J. W. Valentine. 2007. Contrarian clade confirms the ubiquity of spatial origination patterns in the production of latitudinal diversity gradients. Proceedings of the National Academy of Sciences USA 104:18129–18134.

Krug, A. Z., D. Jablonski, J. W. Valentine, and K. Roy. 2009. Generation of Earth's first-order biodiversity pattern. Astrobiology 9:113–124.

Labandeira, C. C., and J. J. Sepkoski, Jr. 1993. Insect diversity in the fossil record. Science 261:310–315.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science, Malden, Mass.

Mannion, P. D., R. B. Benson, P. Upchurch, R. J. Butler, M. T. Carrano, and P. M. Barrett. 2012. A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for Late Cretaceous geographical partitioning. Global Ecology and Biogeography 21:898–908.

Martin, P. R., and J. K. McKay. 2004. Latitudinal variation in genetic divergence of populations and the potential for future speciation. Evolution 58:938–945.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, and H. A. Lessios. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10:315–331.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Naimark, E., and A. Markov. 2011. Northward shift in faunal diversity: a general pattern of evolution of Phanerozoic marine biota. Biology Bulletin Reviews 1:71–81.

Newell, N. D. 1959. Adequacy of the fossil record. Journal of Paleontology 33:488–499.

Novack-Gottshall, P. M., and M. A. Lanier. 2008. Scale-dependence of Cope's rule in body size evolution of Paleozoic brachiopods. Proceedings of the National Academy of Sciences USA 105: 5430–5434.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Payne, J. L., and S. Finnegan. 2007. The effect of geographic range on extinction risk during background and mass extinction. Proceedings of the National Academy of Sciences USA 104:10506–10511.

Powell, M. G. 2005. Climatic basis for sluggish macroevolution during the late Paleozoic ice age. Geology 33:381–384.

——. 2007. Latitudinal diversity gradients for brachiopod genera during late Palaeozoic time: links between climate, biogeography and evolutionary rates. Global Ecology and Biogeography 16:519–528.

——. 2009. The latitudinal diversity gradient of brachiopods over the past 530 million years. The Journal of Geology 117: 585–594.

Powell, M. G., V. P. Beresford, and B. A. Colaianne. 2012. The latitudinal position of peak marine diversity in living and fossil biotas. Journal of Biogeography 39:1687–1694.

Quintero, I., and J. J. Wiens. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. Ecology Letters 16:1095–1103.

Raup, D. M., and J. J. Sepkoski, Jr. 1982. Mass extinctions in the marine fossil record. Science 215:1501–1503.

Renema, W., D. Bellwood, J. Braga, K. Bromfield, R. Hall, K. Johnson, P. Lunt, C. Meyer, L. McMonagle, and R. Morley. 2008. Hopping hotspots: global shifts in marine biodiversity. Science 321: 654–657.

Roberts, C. M., C. J. McClean, J. E. Veron, J. P. Hawkins, G. R. Allen, D. E. McAllister, C. G. Mittermeier, F. W. Schueler, M. Spalding, and F. Wells. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280–1284.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Roy, K., and E. E. Goldberg. 2007. Origination, extinction, and dispersal: integrative models for understanding present-day diversity gradients. American Naturalist 170:S71–S85.

Sepkoski, J. J., Jr. 1978. A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. Paleobiology 4:223–251.

——. 1979. A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. Paleobiology 5:222–251.

——. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. Paleobiology 10:246–267.

——. 1988. Alpha, beta, or gamma: where does all the diversity go? Paleobiology 14:221–234.

——. 1993. Ten years in the library: new data confirm paleontological patterns. Paleobiology 19:43–51.

Sepkoski, J. J., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. Nature 293:435–437.

Sepkoski, J. J., Jr., D. Jablonski, and M. Foote. 2002. A compendium of fossil marine animal genera. Paleontological Research Institution, Ithaca, N.Y.

Stanley, S. M. 1990. The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. Pp. 103–127 *in* R. M. Ross and W. D. Allmon, eds. Causes of evolution: a paleontological perspective. University of Chicago Press, Chicago.

Stanley, S. M., and M. G. Powell. 2003. Depressed rates of origination and extinction during the late Paleozoic ice age: a new state for the global marine ecosystem. Geology 31:877–880.

Stehli, F. G., and J. W. Wells. 1971. Diversity and age patterns in hermatypic corals. Systematic Biology 20:115–126.

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

Tittensor, D. P., C. Mora, W. Jetz, H. K. Lotze, D. Ricard, E. V. Berghe, and B. Worm. 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466:1098–1101.

Valentine, J. W., D. Jablonski, A. Z. Krug, and K. Roy. 2009. Incumbency, diversity, and latitudinal gradients. Paleobiology 34:169–178.

Van Valen, L. M. 1984. A resetting of Phanerozoic community evolution. Nature 307:50–52.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society of London B 275:649–659.

Williams, A., M. A. James, C. C. Emig, S. Mackay, and M. C. Rhodes. 1997. Anatomy. Pp 7–151 *in* A. Williams et al. Brachiopoda 1 (Revised). Part H of R. C. Moore, ed., Treatise on invertebrate paleontology. Geological Society of America, Boulder, Colo., and University of Kansas,Lawrence.

Yasuhara, M., G. Hunt, H. J. Dowsett, M. M. Robinson, and D. K. Stoll. 2012. Latitudinal species diversity gradient of marine zooplankton for the last three million years. Ecology Letters 15:1174–1179.