Symmetric waxing and waning of marine invertebrate genera

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Abstract.—Occurrence data from the Paleobiology Database are used to analyze the waxing and waning of genera over time. Irrespective of whether we tabulate species richness, frequency of occurrence, geographic range, or other measures, the average rise and fall of genera is remarkably symmetrical. Genera tend already to be in a state of decline when they become extinct. Genera that last appear in the major mass extinction stages, however, are more frequently truncated while they are holding steady or even increasing. This need not imply that mass extinctions are qualitatively different from other events; it is consistent with the expected effects of simply increasing the magnitude of extinction. For reasons that are not completely clear, post-Paleozoic genera show less of a rise and fall on average and tend to be less symmetrical than do Paleozoic genera.

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Every taxon varies over time in the magnitude of its presence on Earth, whether this is measured as species richness, geographic range, environmental breadth, or some other quantity. Does this variation show a simple and regular temporal pattern? Are different phases of the history of a taxon—such as the first half versus the second half—predictably different? Such questions are especially salient when we consider major mass extinction events. Do biologic groups tend to be cut down in their prime by major extinction events, or were those groups that became extinct already ''on their way out''?

Miller (1997) showed that Ordovician genera tend to increase in both geographic and environmental range as they age, although he did not document whether ranges systematically change as genera approach their time of extinction. Several studies have documented lower extinction rates for more broadly distributed genera (see Jablonski 2005; Kiessling and Aberhan 2007), but this work generally has not considered the range of a genus at its time of extinction relative to the average range over its entire duration (see Kiessling and Aberhan for an exception).

Here I will use occurrence data from the Paleobiology Database (www.paleodb.org) to show that marine invertebrate genera tend to increase and decrease nearly symmetrically in several quantities, including species richness,

number of collections, number of geologic formations, and geographic range. On average, genera increase toward a maximum and decline from this point at about the same rate they approached it. Thus they tend to be on their way out at the time of extinction. Those that last appear in four of the five major mass extinctions are truncated, however.

Data and Analyses

Occurrence data were downloaded from the marine invertebrate portion of the Paleobiology Database (PBDB) on 21 August 2006. The following options were specified: (1) genus names qualified by ''aff.,'' ''sensu lato,'' or quotation marks were excluded; (2) subgenera were elevated to genus level; (3) genus names were replaced with known senior synonyms. The following data fields were downloaded: (1) collection number, (2) genus name, (3) species name, (4) ordinal name, (5) geologic formation, (6) present latitude and longitude, (7) estimated paleolatitude and paleolongitude, using Scotese's reconstructions (www. scotese.com), and (8) stratigraphic terms (epoch, subepoch, stage, maximum interval, minimum interval, and the PBDB ten-million-year bin). These stratigraphic terms were used, along with correlation charts in Harland et al. (1990) and Gradstein et al. (2004) to place occurrences into a series of operational strati-

graphic bins roughly equivalent to the ''stages'' of Sepkoski (2002) (see Foote 2005).

All told, nearly 330,000 occurrences were downloaded, belonging to over 21,000 genera. An *occurrence* in this context is the unique combination of a genus name and species name in a collection. To help exclude higher taxonomic names that have been incorrectly entered in the genus field, occurrences were discarded if the species field was equal to ''indet.'' For analyses of species richness, a specifically indeterminate combination (*Genus* sp.) was treated as a single species. Combinations such as ''*Genus* sp. A'' and ''*Genus* sp. B'' were treated as distinct species. The raw data file is available in compressed form at the PBDB website (URL: http://paleodb.org/public/repository/Occs. 21Aug2006.csv.gz.ftp).

The following tabulations were then made:

1. *Number of distinct species per genus per stage.* Here, each species was given unit weight regardless of how many collections contain that species.

2. *Number of occurrences per genus per stage.* For this tabulation, each genus in each collection was in effect weighted by the number of species representing it in that collection.

3. *Number of distinct collections per genus per stage.* The presence of a genus in a collection was given unit weight irrespective of how many species of that genus are found in the collection. Because the taxonomic lists for some collections do not include species names at all, accounting for some 28% of the ~330,000 occurrences studied here, this is a more broadly applicable measure of the extent of a genus's presence in the biosphere than either of the first two tabulations, and it will be presented as the principal measure.

4. *Number of distinct formations per genus per stage.* Occurrences lacking a formation name were excluded, and the presence of a genus in a formation was given unit weight regardless of the number of collections of that formation that include the genus.

5. *Number of equal-area cells occupied by the genus per stage.* Paleolatitude and paleolongitude data were used to assign collections to one of 10,000 equal-area cells obtained by taking a Lambert cylindrical equal-area projection, with a primary latitude at 0°, and using 100 latitudinal and 100 longitudinal divisions. The cells are roughly 51,000 km^2, or about the area of a 2° × 2° cell at the equator. Although reconstructed coordinates are uncertain, and generally more uncertain for geologically older collections, this should mainly add noise to the tabulation of occupied cells rather than force a particular trajectory within the history of individual genera. Moreover, the cells are small enough that most are within a single tectonic plate; the number of occupied cells therefore depends mainly on the location of collections on the plates and only secondarily on the positions of the plates. This can be seen by repeating the entire analysis with present-day coordinates, which leads to nearly identical results (not presented).

The steps in analyzing genera over time are illustrated in Figure 1 for a subset of data, namely the genera that first appear in the Tremadocian stage of the Ordovician. All analytical scripts were written in the R programming language (R Development Core Team 2006). In this and all analyses, a genus is included only if its stratigraphic range is three or more stages, although results are consistent if this restriction is relaxed to include all but single-stage genera. With shorter ranges, it would be difficult to discern meaningful temporal patterns. Also, to remove the effects of sparsely sampled genera, many of which are present in their stage of first and last appearance but scarcely in between, genera were retained only if they are found in an average of three or more collections per stage. This minimum is arbitrary, but other choices yield similar results. Similar culling protocols were applied for the other measures (Table 1).

Figure 1A depicts the number of collections per genus for the 97 genera that first appear in the Tremadocian, range through at least three stages, and occur in an average of three or more collections per stage. Each tabulation is depicted as a horizontal line segment extending through the stage. For example, the five bold segments depict the genus *Geragnostus*, which is known from 35 collections in the Tremadocian, 20 in the Arenigian, 9 in the Llanvirnian + Llandeilian, 11 in the Caradocian, and 2 in the Ashgillian. Because all genera in this plot range through at least three stages,
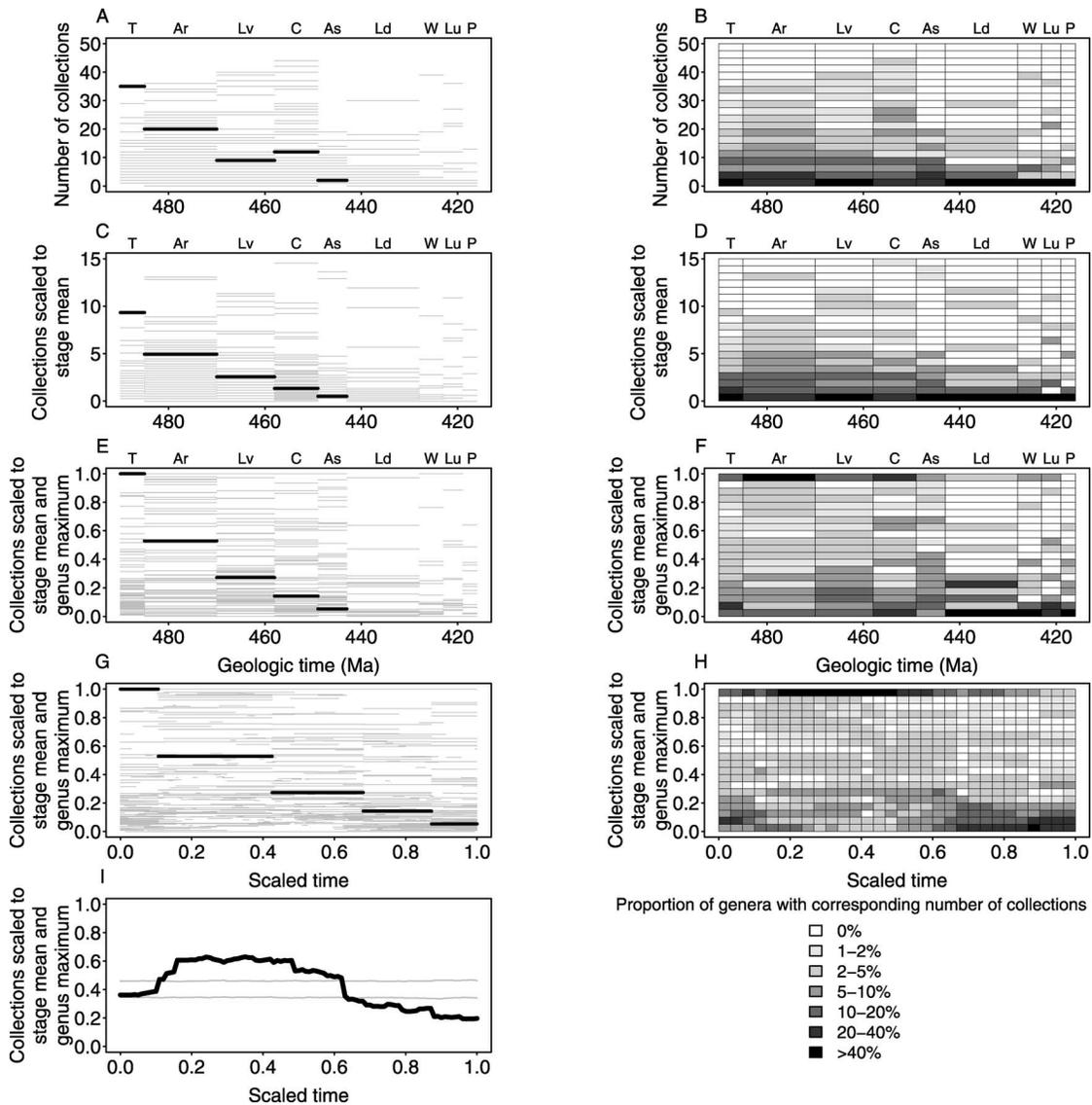
FIGURE 1. Analytical protocols, illustrated with genera that first appear in the Tremadocian. Each horizontal line in A, C, E, and G shows the number of collections within which a genus is found in a stage; lines extend through entire stage. Bold lines are for the genus *Geragnostus*, an arbitrary example. A, Number of collections over geologic time. A few genera have counts higher than 50; these are omitted for clarity. Many genera have identical counts and so are not distinguishable in this figure. B, Number of genera known from a given number of collections in a given stage. Increasing levels of shading indicate that the number of genera is equal to 0%, 1–2%, 2–5%, 5–10%, 10–20%, 20–40%, and >40% of the total for the stage. C, D, Number of collections over geologic time, divided by the mean number per genus for each respective stage. E, F, Number of collections over geologic time, divided by the maximum for each respective genus; this maximum is calculated after first dividing by the mean number per genus for each respective stage. G, H, Same tabulation as in C, with time now scaled for each genus to be 0.0 at the base of the stage of first appearance and 1.0 at the top of the stage of last appearance. I, Mean height of the curves in G (bold line) and the inner 90% of the mean trajectories for 1000 randomizations with respect to time (gray lines). A–F track genera through the end of the Silurian; G–I track genera to their last appearance. Letters at the top of panels A–F denote stage names: T, Tremadocian; Ar, Arenigian; Lv, Llanvirnian + Llandeilian; C, Caradocian; As, Ashgillian; Ld, Llandoverian; W, Wenlockian; Lu, Ludlovian; P, Pridolian.

TABLE 1. Required average quantities to include a genus in analysis.*

Quantity	Minimum value (mean per stage)	Genera retained
Collections	3.0	2030
Occurrences	3.5	1961
Species	1.5	1914
Formations	1.5	1717
Equal-area cells	1.5	2139

* Genus must also have a range of three or more stages to be included.

there are 97 horizontal segments in each of the first three stages, but the number drops off after this. Genera are arbitrarily truncated at the end of the Silurian in Figure 1A, but all inferences are ultimately based upon following genera up to their time of last appearance.

Many genera are known from the same number of collections in a given stage, and so are not distinct from each other in Figure 1A. Figure 1B therefore depicts the relative numbers of genera with shading patterns. A white cell indicates that no genera have the corresponding number of occurrences in the given stage, whereas a black cell indicates that 40% or more of the genera in the given stage are known from the corresponding number of collections. Intermediate shadings are explained in the figure legend.

The overall quantity of data, and therefore the mean number of collections per genus, varies over time. To help account for this, the number of collections for each genus in each stage was divided by the mean number for that stage. The results (Fig. 1C) show a downward adjustment of *Geragnostus* and many other genera in the Caradocian, an interval with an unusually large number of collections overall (see also Miller and Foote 1996). Figure 1D shows the density of occupation in the same way as Figure 1B.

Genera differ from each other in the average number of collections in which they occur, and it is useful to compare them on a common scale of measurement. The number of collections for each genus in each stage, after first being divided by the stage mean, was therefore divided in turn by the maximum over the entire history of the given genus to yield a scaled number of collections varying from 0 to 1. This is depicted in Figure 1E and F.

Finally, to place all genera in a common temporal framework, the duration of each genus was rescaled to unit length from the base of the stage of first appearance to the top of the stage of last appearance (Figure 1G, H). Ages of stage boundaries were based on Gradstein et al. (2004) and on Bowring and Erwin (1998). Results (not presented) are compatible if each stage is treated as having unit length or if the relatively uniform ''10-Myr bins'' of the Paleobiology Database are used instead of the shorter and more variable stages.

It is evident in Figure 1H that the genera in question tend to be known from relatively few collections in about the first 10% and the last 30% of their history, and from relatively more collections in between. This is also seen in Figure 1I, which shows the mean number of scaled collections per genus as a function of scaled time. At each of 100 interpolated, evenly spaced points along the time axis, the height of this thick line is the mean height of all the genera at the corresponding point in time. For comparison, the thin lines show the limits of the upper and lower 5% of mean trajectories obtained by randomizing the scaled collection data with respect to time (1000 iterations). Parts of the average trajectory that fall outside these bounds indicate temporal patterns, including autocorrelation, beyond the expectations of chance variation. This cohort of genera shows an asymmetric trajectory. The average increases to a maximum at a scaled time of just below 20%, stays high for some time, and begins a rather steady wane at about the midpoint of temporal duration. The jaggedness of this and subsequent curves reflects the finite number of ways that stages of given lengths can be combined into stratigraphic ranges.

Results

The pattern of asymmetric rise and fall seen in Figure 1H and I pertains to only a single cohort of genera and is not necessarily representative. Figure 2A shows the same analysis for all Phanerozoic genera. The average also rises and falls conspicuously, but in this case the pattern is nearly symmetric about the temporal midpoint. Other statistics (for example, median number of collections and percentage

of genera that are at their maximum) yield similar results and are not presented here. On average, genera take as much time to decline from their maximum as they do to attain it. Irrespective of the symmetry, genera on average appear to be in a state of decline at their time of extinction.

Figure 2 also depicts the effect of varying the data threshold. As the required number of collections per genus increases, the average trajectory rises and falls more steeply. This effect is related to incomplete sampling. A genus may or may not be present in any of the intervening stages between that of its first and last appearance. But of course it must be present in these two particular stages. This means that the average is biased upward near both ends of the stratigraphic range, which in turn helps account for the flattening of the average trajectories toward the ends. With a lower data threshold, more of the included genera will be relatively sparsely sampled and thus affected by this bias. If no data threshold is imposed, the average trajectory is dominated by first and last occurrences, with little data in between (Fig. 2D).

We see a similar, nearly symmetric rise and fall if we look at other measures (Fig. 3), each one subject to a culling to remove the more sparsely occurring genera (Table 1). The culling criterion in each case was chosen to yield roughly the same number of genera as depicted in Figure 2, but other choices yield similar results. The agreement partly reflects the high correlation between some of the tabulated quantities, for example number of collections and number of occurrences (Table 2), but it holds even for measures that are not highly intercorrelated. Nor is the overall pattern an artifact of scaling to the stage average and the genus maximum, for it is seen even in the unscaled data (results not presented).

The rise and fall of genera is distinctly different for most of the widely recognized mass extinction intervals, however (Fig. 4). Although genera last appearing in the Ashgillian were in decline, on average, at their time of disappearance, the same is not clearly evident for genera that last appear in the Late Devonian, Late Permian, Norian, or Maastrichtian. If anything, genera that last appear in the
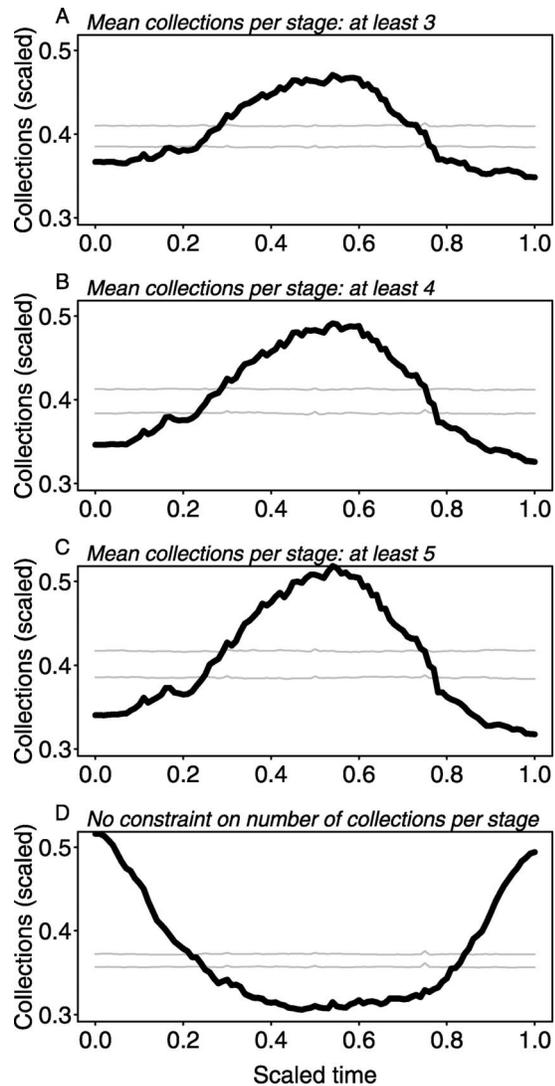
FIGURE 2. Mean and randomized trajectories of the number of collections for all genera included in analysis (see Fig. 1I for explanation). A–C, Results for genera with mean number of collections per stage equal to at least three (A), at least four (B), and at least five (C). Number of collections within which a genus is found tends to rise and fall nearly symmetrically through its history. Rise and fall are steeper when the data threshold is more stringent. D, Results with no minimum number of collections imposed, in which case the average trajectory is dominated by first and last appearances with little in between.

Maastrichtian were generally on their way up and were severely truncated by the Cretaceous/Tertiary extinction event. Taxonomic bias may be a concern here, as turnover can be exaggerated if different systematists study the fauna on either side of a major stratigraphic
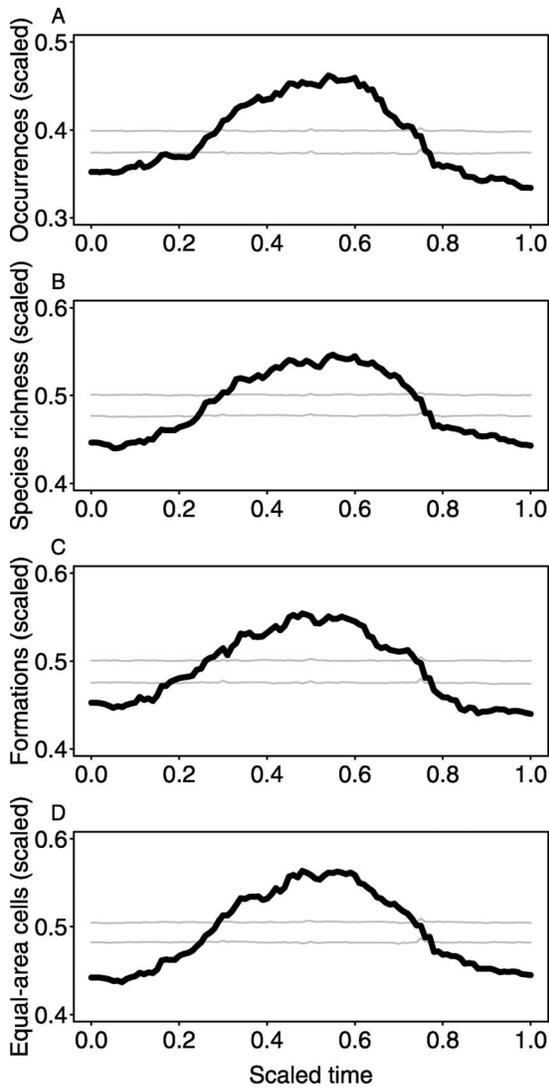
FIGURE 3. Mean and randomized trajectories of other quantities. A, Number of occurrences. B, Number of species. C, Number of formations. D, Number of equal-area cells occupied (with surface of Earth divided into 10,000 cells). All measures show a nearly symmetrical rise and fall.

FIGURE 4. Mean and randomized trajectories of the number of collections for genera that last appear in the five major mass extinction events of the Phanerozoic. Except for the Ashgillian, genera that last appear in these stages tend to make their last appearance while they are relatively stable or increasing.

TABLE 2. Correlations between measures.*

	Occ.	Spp.	Form.	Cells
Coll.	0.99	0.86	0.53	0.91
Occ.		0.89	0.53	0.91
Spp.			0.50	0.88
Form.				0.55

* Spearman rank-order correlations. For each pair of measures, genera are included that have a range of three or more stages and meet data threshold for both measures (see Table 1). Correlation is calculated over all cells in the genus by stage matrix within the stratigraphic range of a genus.

FIGURE 5. Mean and randomized trajectories of the number of collections, comparing genera that last appear in the major mass extinctions (A, B) with all other genera (C). Note scale difference relative to Figure 4. If the Ashgillian is excluded (B), genera that last appear in the mass extinction stages tend to disappear while they are on the increase. D, Average trajectories based on genera that last appear in five randomly chosen stages (100 replicates). The behavior of the genera in A and B is substantially different from most of these random aggregates and therefore outside the expectations of chance variation.

FIGURE 6. Mean and randomized trajectories of the number of collections for genera that last appear in the Visean. This trajectory suggests a truncation similar to that seen in the major mass extinctions.

boundary (Fortey 1989). In this case, however, much the same truncation is seen if the analysis is limited to genera belonging to orders that last appear in the Maastrichtian (according to Jablonski 2002; update personal communication 2006), whose true extinction is presumably not in question (results not presented). Thus taxonomic bias is unlikely to be the cause of the truncation. Because the tabulations in Figure 4 are scaled by the mean number of collections per genus per stage, the upward trajectory toward the Maastrichtian is also unlikely to be an artifact of preferential study of this mass extinction interval.

The numbers are small for some of the sets of genera depicted in Figure 4, and it is not sensible to interpret every peak and valley in these curves. We can see the distinction between the major mass extinctions and other intervals more clearly if we contrast the results for the mass extinctions combined with those for the remaining stages (Fig. 5). On the whole, genera that last appear during these mass extinction stages were not in a state of decline at their time of last appearance. Because of chance variation, the increasing trajectory of Figure 5B could in principle be a fluke. This possibility was tested by generating 100 sets of average trajectories, each one based on the genera that last appear in five different, randomly chosen stages (Fig. 5D). Comparison with these random aggregates shows that the trajectory of the mass extinction victims is anomalous.

In addition to the ''Big Five'' mass extinctions, individual trajectories were constructed for each cohort of first appearances (as in Fig. 1I) and each cohort of last appearances (as in Fig. 4). These are not all presented here, but this exercise shows that genera with last appearances in the Visean may also be truncated more than expected by chance (Fig. 6). This stage is a local peak in extinction in Sepkoski's
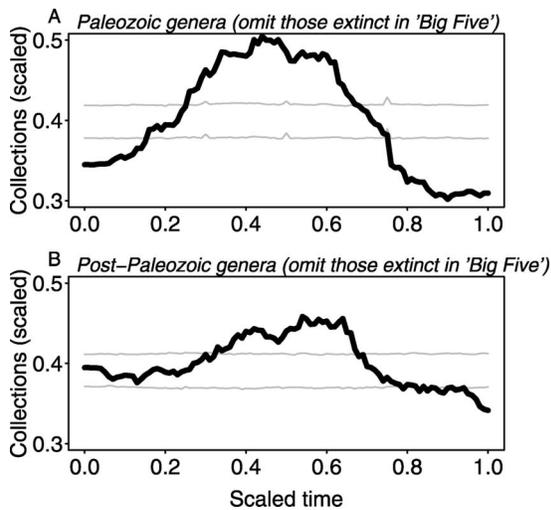
FIGURE 7. Mean and randomized trajectories of the number of collections, comparing genera with first appearances in the Paleozoic versus the post-Paleozoic. The rise and fall of post-Paleozoic genera is more muted and less symmetrical.

(2002) data (Sepkoski 1986), but it is possible that many last appearances in the Visean reflect backsmearing from a Serpukhovian event (Foote 2003, 2007). In any event, given the number of trajectories studied, it is possible that Figure 6 is just a chance anomaly. No obvious patterns stand out with respect to first appearance—for example, a systematic difference for genera that first appear at times of high origination rate—but this question deserves further attention.

Several studies have documented major ecological and evolutionary differences between the Paleozoic and post-Paleozoic biotas (e.g., Sepkoski 1981, 1984; Foote 2000; Miller and Foote 2003; Wagner et al. 2006; Foote 2007). Perhaps it is not surprising, therefore, that the characteristic rise and fall of genera also differs substantially between these two major time intervals. Genera that first appear in the Paleozoic show a clear, and nearly symmetric, increase and decrease, whereas those that first appear in the Mesozoic and Cenozoic show a more muted tendency to rise and fall (Fig. 7), with much of the average trajectory within the expected field for randomized data. In the latter half of the Phanerozoic, genera are more likely to disappear at essentially random points in their history of richness, geo-

graphic range, and so on. Although the reasons for these major differences are not obvious, I will suggest two possible factors below.

Discussion

The principal result of this paper is that the magnitude of the presence of genera, measured in a variety of ways, tends on average to rise and fall symmetrically. Just as genera tend to expand for some time following their first appearance in the fossil record, they tend to be in a state of relative decline at their time of last appearance. At least for species richness, a symmetric rise and fall is perfectly consistent with a time-homogeneous birth-death model (Kitchell and MacLeod 1988) (Appendix). There is substantial variation subsumed within the symmetric average trajectory. Genera that first appear in the Tremadocian, for example, have an asymmetric average trajectory (Fig. 1). Moreover, genera that last appear in the most severe mass extinction stages tend not to be on the wane at their time of disappearance.

The anomalous behavior of genera that disappear in the major mass extinctions (Figs. 4, 5) need not imply that mass extinctions are qualitatively different from background extinctions (see Jablonski 1986; Wang 2003). It stands to reason that a short-lived elevation of extinction rate will truncate genera, that this truncation will be greater if the extinction is more severe, and that it will be especially conspicuous if the extinction event occurs during a time of diversification (as in the Maastrichtian case). These expectations can easily be verified with a simple modification of the time-homogeneous birth-death model (Appendix).

It is not clear why genera that first appear in the Paleozoic show a more striking decline from their peak to their time of disappearance than do post-Paleozoic genera. One contributing factor may be that origination and extinction rates are lower in the post-Paleozoic (Raup and Sepkoski 1982; Van Valen 1984; Foote 2003; Bambach et al. 2004). When species richness within a genus is scaled from zero to one (as in Fig. 3B), the expected amplitude of the genus trajectory is greater as

speciation and extinction rates increase (Appendix).

More speculatively, another factor could be a difference in extinction regimes that has recently been suggested (Foote 2007). According to this view, nearly all stages prior to the Permian have measurable global extinction at the genus level. The Paleozoic thus resembles somewhat the idealized time-homogeneous model, in which symmetric rise and fall is the expectation (Appendix). Starting in the Permian, however, there are long intervals of quiescence, with zero or near-zero extinction rates. These in turn are punctuated by events that are more severe than has generally been thought. Post-Paleozoic genera therefore have more time to expand, diversify, and increase in hubris, only to be cut down in their prime by rare and terrific events. This could help explain the flatness of the end of the average trajectory (Fig. 7B).

Several of the average trajectories (Figs. 1I, 2, 3A, 5C, and 7) are higher at the beginning than at the end. One possible reason for this concerns the relative fidelity of origination and extinction. Foote (2003) suggested that, for marine animal genera, there tends to be a greater offset between true origination and first appearance than between extinction and last appearance (see also Peters 2005; Lu et al. 2006). This implies that many genera may have had substantial time to accumulate species, disperse geographically, and so on, before their first appearance. Conversely, there would have been less time to wane after their last appearance. In other words, the average trajectory may be artificially truncated to a greater extent at the beginning than at the end.

It is unlikely that the regular rise and fall of genera is an artifact of sampling. Bearing in mind that measures have been adjusted for variation in the quantity of data from stage to stage, a genus tends to have more sampled species and a wider sampled geographic range at a given time because it really was more species rich and more widespread at that time. The rise and fall of genera can be thought of as a rise and fall in sampling probability, but only because this in turn is largely dictated by biologically meaningful quantities such as numerical abundance, species richness

and geographic range. The rise and fall of genera suggests that the offsets between origination and first appearance and between extinction and last appearance are often greater than they would be if these biological properties—and thus sampling probability—were constant. The extent to which this affects efforts to infer true durations, diversity, and turnover rates (Miller and Foote 1996; Alroy et al. 2001; Connolly and Miller 2001; Holland 2003; Foote 2001, 2003, 2005; Chen et al. 2005; Crampton et al. 2006a,b) remains to be seen.

A previous analysis of geographic range in Triassic and Jurassic invertebrates also found that genera tend to be below their peak when they disappear from the record, although that study, unlike the present work, reported a tendency for maximum range to be attained early (Kiessling and Aberhan 2007). Is it at all surprising or noteworthy that genera are below their maximum early and late in their history? At the one end, a genus—to the extent that it is a phylogenetic unit (Jablonski et al. 2006)—must start with a single species in a relatively restricted region, and can go nowhere but up, at least initially. At the other end, several studies have shown that geographic range often increases the chances of survival (see survey in Jablonski 2005; Kiessling and Aberhan 2007), although species richness may not be an important selective factor for some groups during the major mass extinctions (see Jablonski 1995).

Here it is important to bear in mind that preferential extinction of genera that are less diverse and widespread *than other genera* at a point in time is not necessarily the same as preferential extinction of genera that have declined *relative to some prior state.* For example, geographic range contributes to survival through many mass extinction events (Jablonski 2005), but the genera that last appear at most of these events are not systematically on the wane (Figs. 4, 5).

Whereas the rise of genera may be entirely expected, the tendency to decline regularly toward the time of extinction is not a foregone conclusion. Moreover, what is so striking about the average trajectory for Phanerozoic genera is the comparative *symmetry* in their rise and fall (Fig. 2).

Other than the fact that symmetric trajectories are predicted by basic branching theory (Appendix), it is not clear why genera should have such a regular pattern on average. One reviewer suggested that the rise and fall of genera is predictable as a consequence of taxonomic practice. Assume species are assigned to genera on the basis of phenotypic similarity. As the genus evolves, the descendants of its founding member will tend to be ever less similar to the founder and therefore less likely to be recognizable as phylogenetically related. What this would do in effect is to add species-level pseudoextinction to true lineage termination in the branching model (Appendix). An open question concerns the relative importance of true extinction and pseudoextinction at the species level.

Of course a complete model of the waxing and waning of genera would ultimately have to include many additional factors such as geographic dispersal, numerical abundance, and sampling probability. What calls especially for attention is why quantities other than species richness also rise and fall symmetrically. Theory on the temporal variation in geographic range does not yet seem sufficiently well developed (Gaston 2003) to make sense of this symmetry. Any process that produces increases and decreases in a quantity of interest, such as geographic range, at stochastically constant rates should lead to patterns similar to those predicted for species richness by the simple branching model.

It is unclear to what extent patterns of waxing and waning vary systematically among taxonomic levels. Dowsett (1989) found that a sample of Pliocene species of planktonic foraminifera and calcareous nannofossils were more diachronous in their first appearances than their last appearances. This suggests that it took species a longer time to spread throughout their geographic ranges than it did for them to become extinct throughout their ranges—a ''top-heavy'' average trajectory. Jablonski (1987) inferred that many Late Cretaceous molluscan species reached their maximal geographic ranges fairly early in their history, suggesting a ''bottom-heavy'' or flat average trajectory. On the other hand, limited data on site occupancy in late Cenozoic

mammal species from Italy (Raia et al. 2006) agree with genus-level data from a larger Neogene sample (Jernvall and Fortelius 2004) in showing a conspicuous rise and fall in occupancy.

Webb and Gaston (2000) reported a variety of relationships between inferred age and geographic range of living bird species. Because Webb and Gaston's analyses do not track species to their time of extinction, they do not compare readily with the analyses presented herein.

Moving to a higher taxonomic level, Gould et al. (1977, 1987) reported that orders tend to be bottom-heavy in terms of family level diversity. Analyses not presented here reveal a similar bottom-heavy pattern of collections, occurrences, and geographic range within orders. Because most of the orders with sufficient data to be analyzed first appear in the lower Paleozoic, it is not clear to what extent the asymmetry is a reflection of taxonomic level versus time of origin.

At any taxonomic level, it may be unwise to generalize from limited analyses. As shown here, genera that first appear in the Tremadocian buck the general trend in tending to be bottom-heavy, and Kiessling and Aberhan (2007) reported a tendency for Triassic and Jurassic genera to reach their maximum geographic range early. Likewise, it remains to be seen whether the species-level results of Dowsett (1989), Jablonski (1987), or Raia et al. (2006) are most representative.

Summary

1. Within Phanerozoic marine invertebrates, genera on average rise and fall nearly symmetrically over their durations. This is the case whether we consider frequency of occurrence, species richness, or geographic range. As expected under the time-homogeneous branching model, genera tend to be ''on their way out'' at their time of last appearance.

2. Genera that last appear in the major mass extinction stages are not so far below their maximum when they disappear. Rather, they are truncated at seemingly random points in their individual trajectories. This need not imply that these mass extinctions are qualitatively different from less severe events.

3. Post-Paleozoic genera show a less pronounced rise and fall than do Paleozoic genera. This may in part be related to a different extinction regime, in which long periods of quiescence are punctuated by very severe extinction events, and in part to lower speciation and extinction rates compared with the Paleozoic.

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Appendix

Expected Trajectory of Species Richness Within a Clade

The expected shape of clades has been explored by Monte Carlo simulation (Gould et al. 1977; Kitchell and MacLeod
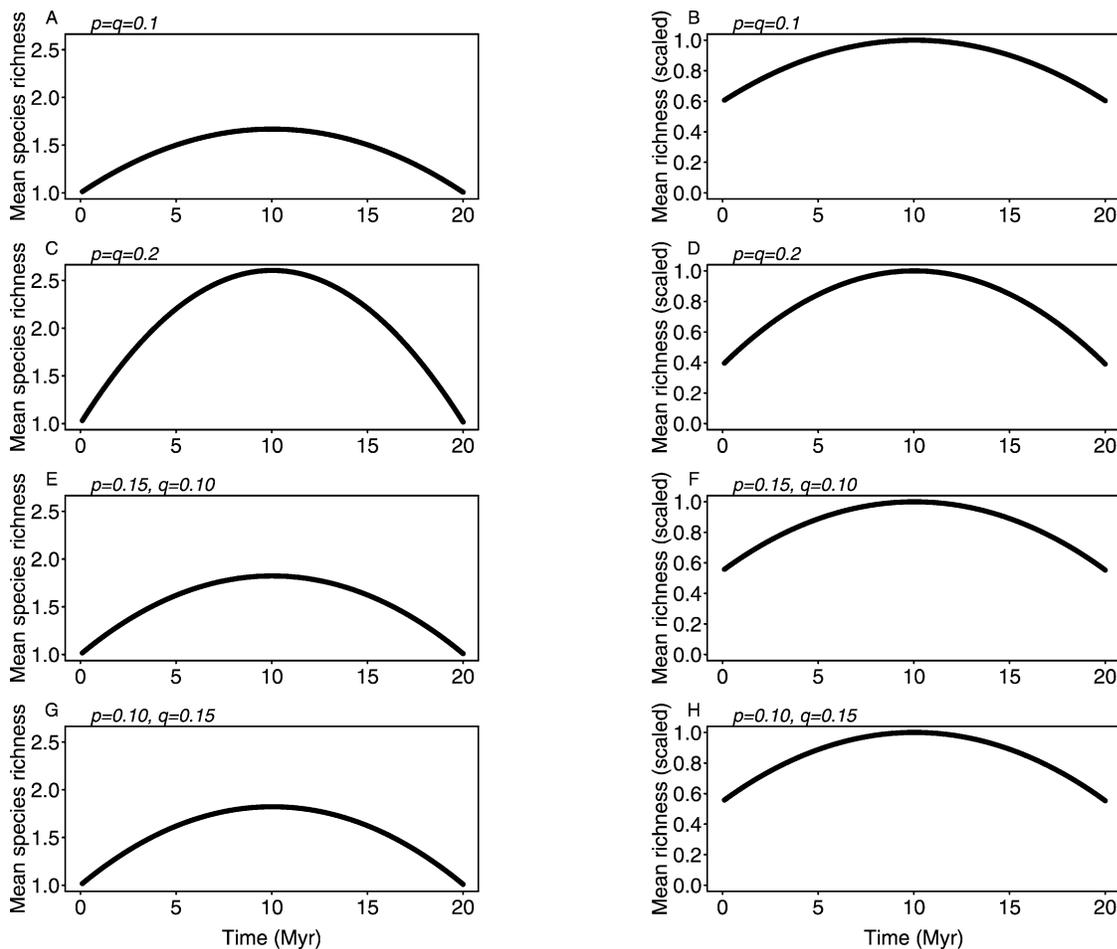
FIGURE A1. Mean species richness within a clade, conditioned on clade origination at $t = 0$ and extinction between $t = T$ and $t = T + \delta t$. Here $T = 20$ Myr and $\delta t = 0.1$ Myr, and origination rate (p) and extinction rate (q) are varied. A–D, $p = q$. E, F, $p > q$. G, H, $p < q$. Left-hand panels show absolute richness; right-hand panels show richness scaled to the genus maximum. In all cases the expected trajectory is symmetrical. Higher speciation and extinction rates produce scaled trajectories with a greater amplitude.

1988), including such features as temporal variation in origination and extinction rates and diversity-dependence of rates. Here it is treated analytically for the simple time-homogeneous, non-equilibrial case (the ''freely floating'' model of Gould et al. 1977).

Let p and q be the per-capita rates of origination and species extinction per lineage-million-years, and assume these are constant over time. We would like to know the expected species richness within a clade at time t, given extinction within a small time increment between T and $T + \delta t$. The following expressions are needed (all derived from Raup 1985).

- The probability of extinction of the clade at or before time x, starting with an initial diversity of a ($a \geq 1$):

$$P_{a,0,x} = \begin{cases} [px/(1 + px)]^a, & \text{if } p = q; \\ \left[\dfrac{q\{\exp[(p - q)x] - 1\}}{\{p \exp[(p - q)x] - q\}} \right]^a, & \text{if } p \neq q. \end{cases}$$

- The unconditional probability of extinction between time T and time $T + \delta t$, assuming a starting diversity of a ($a \geq 1$):

$$P_{a,0,T,T+\delta t} = P_{a,0,T+\delta t} - P_{a,0,T}$$

- The probability that standing diversity of the clade at time t is equal to n, given that $n > 0$ and that the clade starts with a single lineage:

$$P_{n,t} = \begin{cases} \dfrac{pt^{(n-1)}/[1 + pt^{(n+1)}]}{1 - P_{1,0,t}}, & \text{if } p = q; \\ (1 - pP_{1,0,t}/q) \cdot (pP_{1,0,t}/q)^{(n-1)}, & \text{if } p \neq q. \end{cases}$$

- The probability that diversity is equal to n at time t ($n > 0$) and that the clade becomes extinct between time T and time $T + \delta t$ ($t < T$):

$$P_{n,t,0,T,T+\delta t} = P_{n,t} \cdot P_{n,0,T-t,T-t+\delta t}$$

- The probability of extinction between time T and time $T + \delta t$, given that the clade is extant (i.e., $n > 0$) at time t ($t < T$):

$$P_{s,t,0,T,T+\delta t} = \sum_{n=1}^{\infty} P_{n,t} \cdot P_{n,0,T-t,T-t+\delta t}.$$

- The probability that diversity is equal to n at time t ($n > 0$), given that the clade becomes extinct between time T and time $T + \delta t$ ($t < T$):

$$P_{n,t0,T,T+\delta t} = P_{n,t,0,T,T+\delta t} / P_{s,t,0,T,T+\delta t}$$

From this last expression we obtain the expected standing diversity at time t, given extinction between T and $T + \delta t$ ($t < T$) as

$$E_{n,t|0,T,T+\delta t} = \sum_{n=1}^{\infty} n \cdot P_{n,t|0,T,T+\delta t}.$$

The expectation is plotted in Figure A1 for $T = 20$ Myr, $\delta t = 0.1$ Myr, and several values of p and q. Note that the expected trajectory is symmetric regardless of whether origination rate is less than, equal to, or greater than extinction rate. This result is not peculiar to the particular parameter values used here. One might have expected asymmetry for the cases where $p \neq q$—for example, top-heaviness for $p > q$. This is not the case because the expected richness is conditioned on a particular time of extinction. For a given set of stochastically constant rates, most genera may indeed be on the rise, but this will not generally be true for the subset that become extinct at a specified time. Note also that, for any given rates a and b, the expectation is the same
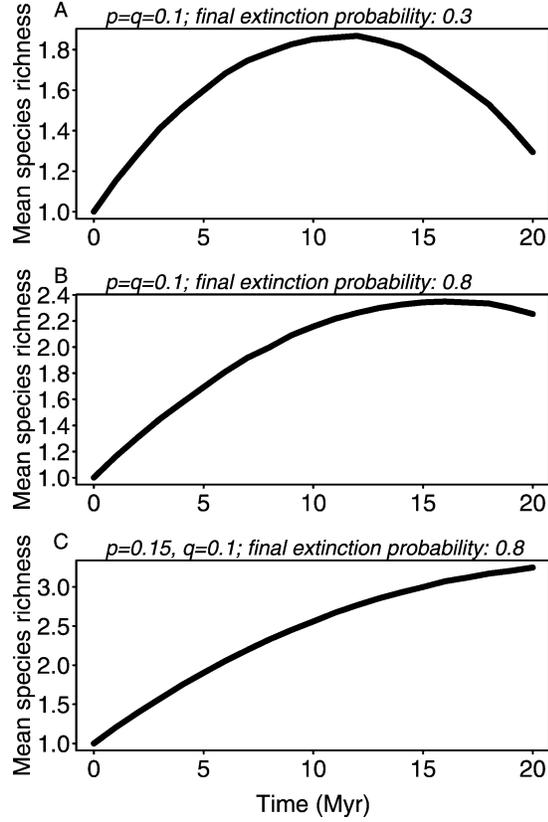
FIGURE A2. Mean species richness within a clade, conditioned on clade origination at $t = 0$ and extinction at $t = T$, where there is a short-lived extinction event at time T. Results are based on discrete-time branching simulations (see Gould et al. 1977; Kitchell and MacLeod 1988), with a constant probability of origination (p) and extinction (q) per time step up to time T. At time T, each species has a fixed probability of becoming extinct. If all the species become extinct at this time, then the clade is extinct and its diversity history is tabulated. Each trajectory shows the mean diversity history of 10,000 simulated clades that became extinct at time T. A, When the increase in extinction probability is moderate, the clade shows an asymmetric trajectory but is still likely to be in a state of decline leading up to its extinction. B, When the increase in extinction probability is severe, the clade shows a truncated trajectory. C, The truncation is even more pronounced if the clade is diversifying up to its time of extinction (i.e., if origination rate exceeds extinction rate).

for ($p = a$, $q = b$) as for ($p = b$, $q = a$). This makes sense because the coalescence of lineages backward in time is mathematically the same as the splitting of lineages forward in time. If species richness is scaled to the maximum for the genus, higher speciation and extinction rates lead to trajectories with greater amplitude.

Time-inhomogeneous cases are easily explored with stochastic simulation (Gould et al. 1977). In Figure A2, for example, there is a single perturbation at a specified time, leading to a truncation of the average trajectory.