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Michael Foote and Arnold I. Miller

Abstract.—Genera by their very nature are expected to be monotypic and geographically and environmentally restricted at their origin, and most genera do not endure past their stage of first appearance. At the same time, those genera that do endure have a capacity to expand greatly in geographic range, environmental breadth, and species richness. Here we ask what it is that allows some genera and not others to survive past their inception. Using occurrence data from the Paleobiology Database, we find that initial geographic range has the strongest effect on survival, followed by environmental breadth, with the effect of species richness weaker on average. The effect of geographic range is strongest if measured as the distances spanned by the occurrences of a genus rather than the number of distinct areas in which a genus lives. We document substantial secular variation in selectivity of early survival. The most striking aspect of this variation is that survival is only weakly selective among genera that first appear during the Mesozoic. By following genera beyond their stage of first appearance, we find that selectivity with respect to all factors becomes systematically stronger as cohorts age and genera become more differentiated in range, breadth, and richness. This may help account for a previously identified statistical effect of genus age on the chances of survival.

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Why Do Some Genera and Not Others Survive Well Past Their Time of Origin?

Species and genera are geographically restricted at their inception, and in general expand in geographic range as they age, contract in range to become restricted once again, and then become extinct (Willis and Yule 1922; Willis 1926; Miller 1997; Jernvall and Fortelius 2004; Raia et al. 2006; Liow and Stenseth 2007; Foote 2007; Foote et al. 2007, 2008; Liow et al. 2010). The extent to which this regular pattern reflects the simple expectations of a random walk (Foote 2007; Pigot et al. 2012), ecological interaction (Liow and Stenseth 2007), or other factors remains unknown. But why do some genera and not others even have a long-term history to speak of? About half of marine animal genera last no more than a single stratigraphic stage (Fig. 1A). Moreover, the majority of genera in their first stage exhibit the minimum possible values of several factors that contribute to survival; they consist of a single species in a single environmental zone with the smallest possible geographic range (Fig. 1B–D) (see *Materials and Methods*). There is

nonetheless appreciable variance among genera, as some do manage to expand and diversify, even within their stage of first appearance. What we would like to ask, then, is (1) which, if any, characteristics of genera, *in the earliest part of their history*, determine whether they will escape “infant mortality” and endure beyond their stage of first appearance, and (2) what is the relative importance of these factors? The factors we consider—geographic range, environmental breadth, and species richness—are all thought to contribute to survival in general (Jackson 1974; Hansen 1980; Jablonski 1986, 1987, 2005; Baumiller 1993; Kammer et al. 1997, 1998; Jablonski and Hunt 2006; Kiessling and Aberhan 2007; Payne and Finnegan 2007; Powell 2007; Finnegan et al. 2008; Harnik 2011; Heim and Peters 2011), but their contribution to the earliest history of lineages has not been a major focus of previous research (see Liow et al. 2010, however). By comparing the probability of survival with the range, breadth, and richness attained in the first stage of a genus’s existence, we are in effect probing the influence on long-term

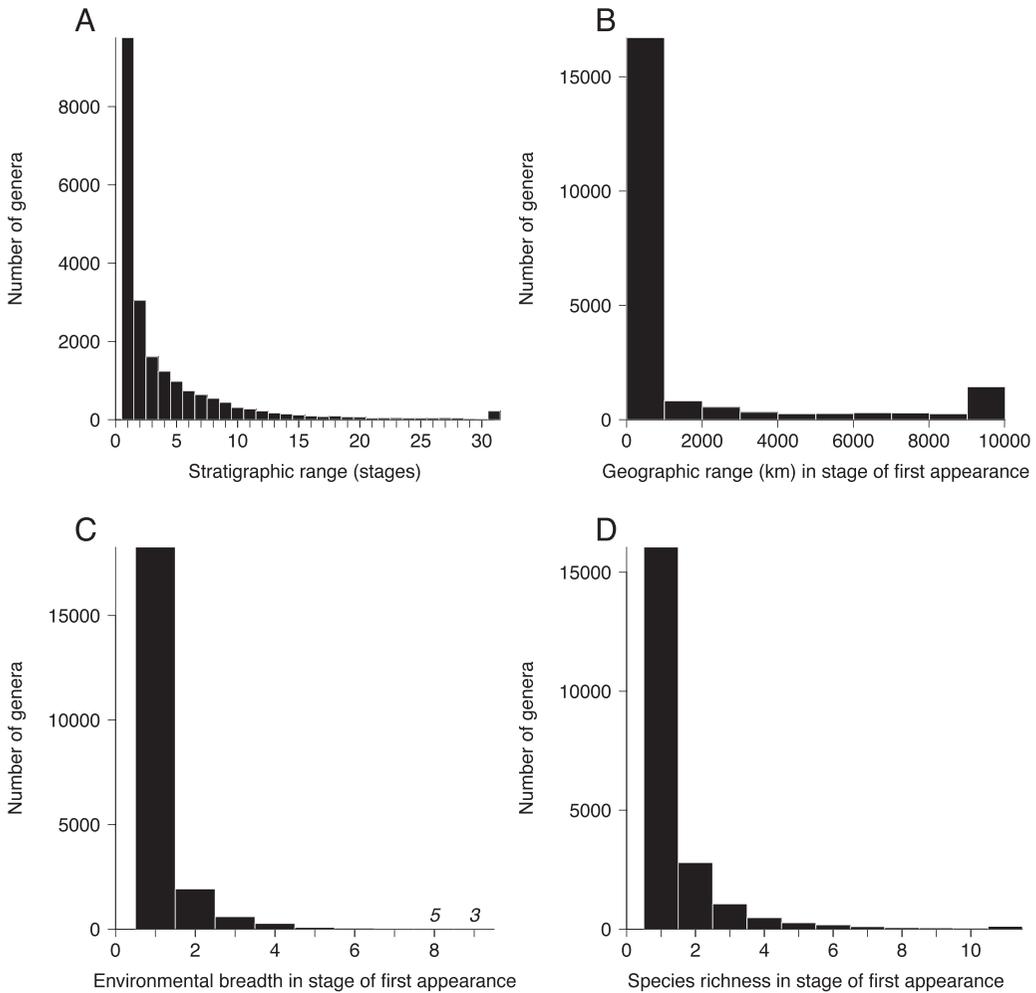


FIGURE 1. Frequency distributions of genus stratigraphic ranges (A), and of geographic range (B), environmental breadth (C), and species richness (D) of genera in their stage of first appearance. Distributions are highly skewed, and most genera are short lived, geographically and environmentally restricted, and species poor. Right-most bars in A, B, and C include values above maximum of abscissa.

survival of the initial rate of increase of these factors.

Materials and Methods

Raw Data.—We downloaded data on occurrences of marine animal genera from the Paleobiology Database (<http://paleodb.org>) on 23 February 2012. To restrict the download to marine animals and environments, we excluded collections known to be from terrestrial and freshwater environments, included only occurrences of Metazoa, and excluded occurrences of Tetrapoda except for certain marine tetrapod groups such as Cetacea (following Hannisdal and Peters 2011). We

excluded form taxa, ichnotaxa, and genus occurrences qualified by “aff.,” “cf.,” “ex gr.,” “sensu lato,” “?,” “informal,” and quotation marks. We employed the options to replace names with senior synonyms and to elevate subgenera to genus rank. In addition to taxonomic names, we downloaded environmental, lithologic, and stratigraphic information, and inferred paleolatitude and paleolongitude, based on Christopher Scotese’s reconstructions as implemented by the Database (C. Scotese personal communication to Paleobiology Database 2001).

Following the initial download of 577,855 occurrences in 83,365 collections, we vetted

data in an effort to remove principally non-marine groups that were included in marine collections, such as insects, unionid bivalves, and basommatophoran gastropods, as well as a small number (84) of evidently terrestrial and freshwater collections. These are legacy collections from the affiliated *Evolution of Terrestrial Ecosystems* project (Behrensmeyer et al. 1992; <http://www.mnh.si.edu/ete/>) that were subsequently incorporated into the Paleobiology Database. They passed our environmental filtering either because they have no term entered in the environment field or because they have a term such as “deltaic” that is ordinarily meant to be applied to marine deposits in the Database. We identified potential homonyms by finding genus names that are assigned to more than one higher taxon. For example, the genus name *Kinkaidia* may apply to a gastropod (Thein and Nitecki 1974) or a rugose coral (Easton 1945). All told, there were 19,738 occurrences of potential homonyms. Many such instances, however, appear to reflect alternative taxonomic opinions rather than homonymy. For example, the genus *Protomegastrophia* (Caster 1939) is assigned variously to the families Leptostrophidae and Strophodontidae. Such instances, many of which reflect ambiguities that arise when subgenera are elevated to genus rank, account for 17,521 of the 19,738 initially flagged occurrences. The occurrences of potential homonyms were further inspected to determine whether the age and context of the collection are consistent with the prospective taxonomic assignment. For example, the genus name *Reubenella* could refer to either a trilobite (Lochman 1966) or an ostracode (Sohn 1968); one particular occurrence is assigned to the Ostracoda by the taxonomic scripts of the Database but is in a collection (number 287) linked to the paper (Lochman 1966) in which the trilobite genus was originally described, so we reassigned this occurrence to the trilobite genus *Reubenella*. This and similar instances account for only 111 occurrences. Finally, we removed 826 collections lacking estimated paleo-coordinates. After all steps in the vetting were completed, there remained 570,139 occurrences of 25,201 distinct genera in 82,048 collections.

Stratigraphic Assignment.—We assigned occurrences to stratigraphic intervals, mainly stages, based on information in the stratigraphic fields. The Ordovician was divided into the five “11-million-year” intervals (Alroy et al. 2008) of the Paleobiology Database, which correspond to the series of the “old” British Standard (Fortey et al. 1995). We are currently using biostratigraphic and other information to assign Ordovician collections to international stages (Ogg et al. 2008), but that task is not yet completed. Given the general concordance between results using stages and coarser time bins for other intervals (see Fig. 6 and Appendix 2), we expect that our conclusions would not be materially altered by using the newer, more highly resolved, Ordovician stages. The Silurian was divided into epochs. The Paleocene, Eocene, and Miocene were divided into subepochs, and the remainder of the Cenozoic was resolved at the epoch level. (For simplicity we will hereinafter refer to all intervals as *stages*.) In total, 519,197 occurrences of 24,302 genera in 73,677 collections could be stratigraphically resolved. (Raw data are available as Supplementary Table 1.) Because of relatively low stratigraphic resolution in the Cambrian, we did not analyze genera with first appearances before the Ordovician. Furthermore, because there are relatively few Holocene collections in the Paleobiology Database, survival of genera originating during the Pleistocene cannot be tracked well, and apparent survivorship is artificially low. If we take the data at face value, it appears that only 11.3% of genera with Pleistocene first appearances survived past this epoch (Fig. 2), the lowest value for any time period, even lower than the major mass extinctions. The face-value Pliocene figure is also rather low. To be conservative, we therefore restricted analysis to 21,225 genera with first appearances from the Ordovician to Miocene. We have repeated analyses with the Pliocene and Pleistocene genera included and found that our substantive conclusions are unaffected (results not presented).

Geographic Range, Environmental Breadth, and Species Richness.—We tabulated the range, breadth, and richness of each genus within

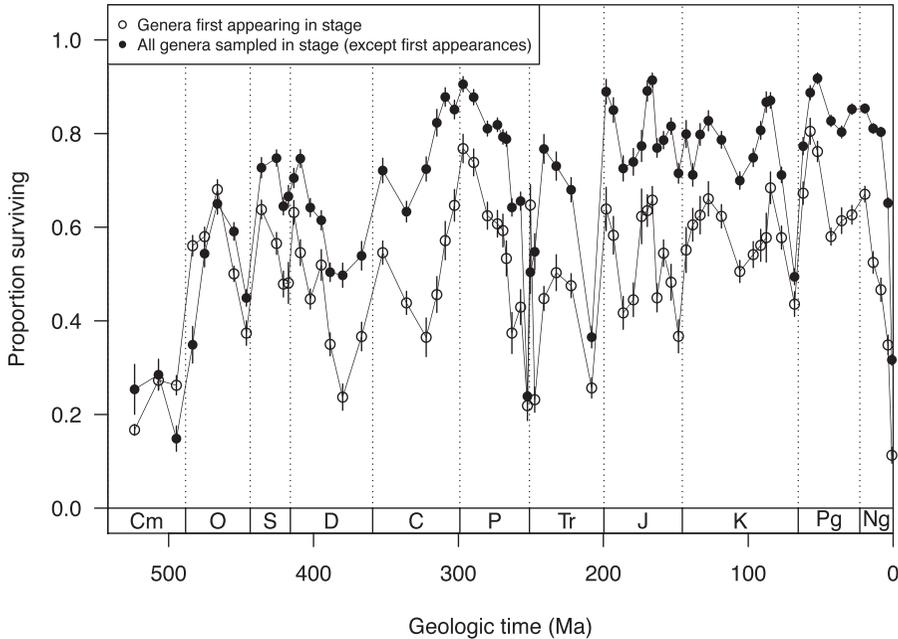


FIGURE 2. Proportion of genera within each stage that survive at least until the next stage. Genera first appearing in a stage are contrasted with those carrying over from the prior stage; only those carryover genera actually sampled in the stage are included. Note the low values for the Pliocene and Pleistocene (the last two points in the time series), which are probably artifacts of the small number of Holocene collections in the Paleobiology Database. In most stages, established genera survive preferentially relative to new genera, but new genera have higher survivorship in the later Cambrian, the Early and Middle Ordovician, and the Early Triassic (Induan stage).

each time interval. We initially measured geographic range in four ways: as the latitudinal range; longitudinal range; maximum great-circle distance between the two most distant occurrences of a genus; and the number of equal-area cells occupied by the genus after projecting all paleolatitudes and -longitudes into a Lambert cylindrical equal-area projection and dividing the map with a 100×100 latitudinal by longitudinal grid. These cells are very roughly 5×10^4 km² in area.

We measured environmental breadth as the number of distinct environmental zones occupied by a genus. Using terms in the environment field and the explanation of environmental settings at the Database website (<http://paleodb.org/public/tips/environtips.html>), we assigned occurrences to one of 11 environmental zones that reflect both an onshore-offshore gradient (Jablonski and Bottjer 1988; Miller 1988; Sepkoski 1988; Holland and Patzkowsky 2007) and overall carbonate versus terrigenous clastic depositional setting (Table

A1). We did not take lithology explicitly into account, although it is the case that primary lithologies (carbonate versus clastic) tend to match their depositional settings fairly well (Table A2). We find similar results with a sixfold environmental zonation that ignores overall carbonate versus clastic depositional setting (see below). Our sixfold scheme agrees in many respects with that of Heim and Peters (2011; corrections by N. A. Heim personal communication 2011), although there are appreciable differences (Table A1), but we also find similar results with Heim and Peters's scheme (see below). We ignored unknown or unspecified environments except that when none of the occurrences of a genus within a stage could be resolved to specific zones, the genus was assigned a minimal environmental breadth of one zone for that stage. Because they lack sufficient information, 55% of collections could not be assigned to environmental zones (Table A2). This number varies from lower values of 31% in the Ordovician and 39% in the Jurassic to highs of 71%, 63%, 62%, and 67% in the

TABLE 1. Spearman rank-order correlations between genus properties in stage of first appearance.

	Species	Environments	Equal-area cells	Great-circle distance	Latitudinal range	Longitudinal range	Convex-hull area
Environments	0.301						
Equal-area cells	0.553	0.520					
Great-circle distance	0.549	0.492	0.907				
Latitudinal range	0.548	0.494	0.910	0.990			
Longitudinal range	0.548	0.490	0.903	0.995	0.981		
Convex-hull area	0.420	0.374	0.837	0.898	0.872	0.884	
Collections	0.538	0.504	0.780	0.842	0.838	0.840	0.424

Permian, Cretaceous, Paleogene, and Neogene. The remaining periods are close to average: 52%, 52%, 53%, and 56% in the Silurian, Devonian, Carboniferous, and Triassic, respectively. Although these numbers strike us as high, there is no clear reason to think that missing data produce an inherent bias toward the results we document. As shown below, we obtain compatible results when we disregard genera lacking assignable occurrences. Moreover, we find only a weak correlation between the proportion of unassigned collections and the strength of association between environmental breadth and survival, measured as the log odds ratio (see next section); the Spearman rank-order correlations (r_s) are $r_s = -0.12$ ($p = 0.76$) and $r_s = 0.15$ ($p = 0.22$) if data are aggregated at the system and stage level of resolution, respectively.

We determined the minimum number of species per genus by tabulating the number of distinct names in the species field for each genus. We ignored the strings “sp.” and “spp.” except if these were the only fields entered for a particular genus in a stage; in that case the genus was assigned a minimal richness of a single species for that stage. Designations such as “sp. 1” or “sp. A” were treated as valid species. Although this protocol could be questioned, it should have little bearing on our results, as such instances account for fewer than 0.1% of all occurrences in the data.

The growth in geographic range of genera is associated with an expansion in environmental breadth (Miller 1997) and species richness (Foote 2007; Krug et al. 2008). Although these measures are positively correlated, the correlations are not sufficiently strong as to make the measures redundant (Table 1), and it is

therefore worth analyzing geographic range and environmental breadth separately. If we focus on the stage of first appearance, we see that three distance-based measures of geographic range—latitudinal range, longitudinal range, and maximal great-circle distance between occurrences—are all highly correlated with each other and with the number of equal-area cells occupied (Table 1). We chose as our principal measure of range size the maximal great-circle distance, since it incorporates both latitudinal and longitudinal extent. We will explore other measures below.

Abundance is an ecological factor that is sometimes considered relevant to survival of species and genera on geological timescales (Lockwood 2003; Simpson and Harnik 2009; Harnik 2011; Payne et al. 2011; Harnik et al. 2012). We chose not to analyze abundance mainly because so few (~27%) of the Paleobiology Database collections in this study include abundance data. In one analysis below, we will consider an indirect proxy for abundance, namely the number of distinct collections in which a genus occurs.

Strength of Selectivity.—The distributions of geographic range, environmental breadth, and species richness are all highly skewed, with the majority of genera having the minimal possible value in their stage of first appearance (Fig. 1). A reasonable approach to evaluating the importance of the variates with respect to survival beyond the first stage is simply to tally, in the form of a 2×2 table, the survival versus extinction of genera with values at or below the median versus values above the median (Table 2). Let N_{ij} be the number of genera in row i and column j of the table, where $i = 1$ and $i = 2$ denote a quantity at or below the median versus one above the

TABLE 2. Survivorship with respect to genus properties. *Restricted*, *narrow*, and *poor* refer to genera with values less than or equal to the median; *widespread*, *broad*, and *rich* refer to genera with values greater than the median.

	Genera not surviving to next stage	Genera surviving to next stage	Probability of survival	Odds of survival	Odds ratio	Log odds ratio	Standard error
Geographic range							
Restricted	6085	6192	0.504	1.018			
Widespread	3678	5270	0.589	1.433	1.408	0.342	0.0281
Environmental breadth							
Narrow	8720	9554	0.523	1.096			
Broad	1043	1908	0.647	1.829	1.670	0.513	0.0413
Species richness							
Poor	7562	8497	0.529	1.124			
Rich	2201	2965	0.574	1.347	1.199	0.181	0.0323

median, and $j=1$ and $j=2$ denote extinction in the stage of first appearance versus survival past the stage of first appearance. Then the probability of survival given i is equal to $N_{i2}/(N_{i1}+N_{i2})$; the odds of survival given i is equal to the probability of survival divided by the probability of extinction, which is equal to N_{i2}/N_{i1} ; and the odds ratio expressing the effect of the level of i (e.g., geographically restricted versus widespread) on the odds of survival is equal to $(N_{11}N_{22})/(N_{12}N_{21})$. It is conventional to express this ratio as its natural logarithm; the standard error of the log odds ratio is then approximately equal to $\sqrt{(1/N_{11} + 1/N_{22} + 1/N_{12} + 1/N_{21})}$ (Agresti 2007: p. 30). These tabulations suggest that the increase in the odds of survival is somewhat greater if a genus has an above-average environmental breadth than if it has an above-average geographic range or above-average species richness (Table 2).

Before we stick our necks out and interpret the result that selectivity is strongest with respect to environmental breadth, we should point out that this analysis is potentially misleading, because the quantities in question are not distributed in the same way. In their stage of first appearance, some 86% of genera are confined to a single environmental zone, 58% of genera have the minimum (and median) geographic range of zero, based on distance measures (i.e., they are found in a single collection or multiple collections with the same coordinates), and 76% of genera have a single species. Thus, for environmental range, we are contrasting the effect of being in the lower 86th percentile versus the upper 14th percentile, whereas the contrasts are less

extreme in the case of geographic range or number of species. It therefore stands to reason that we might expect a stronger effect of environmental breadth based solely on differences in the respective distributions. It is hard, without begging the question, to say how much of an increase in species richness or geographic range should be considered comparable to a unit increase in environmental breadth. We therefore use a method akin to quantile normalization (Bolstad et al. 2003) to transform the distributions of geographic range and species richness so that they are distributed like environmental breadth, which serves as the reference distribution.

We apply the normalization as follows: Because the maximal, realized environmental breadth for genera in their stage of first appearance is nine zones, each of the other two distributions is divided into nine ordered categories. We see that 86.2% of genera are confined to a single environmental zone, 9.0% are found in two zones, and so on (Table 3). Therefore, the genera with the smallest 86.2% of the geographic ranges are assigned a normalized geographic range of 1, the next largest 9.0% are assigned a normalized range of 2, and so on. In this way, the distributions of geographic range and environmental breadth are made identical, although information is lost because distinctions among geographic range in the same normalized bin are no longer made. Species richness is normalized similarly, although, because of the discrete nature of this variate, the boundaries between quantiles cannot be set so as to achieve exactly the same statistical distribution as for envi-

TABLE 3. Normalized variates.

Environmental breadth			Geographic range (great-circle distance)		No. of species	
Quantile	No. of zones	Proportion of genera	Lower limit (km)	Proportion of genera	Lower limit	Proportion of genera
1	1	0.862	0	0.862	1	0.757
2	2	0.090	3663	0.090	2	0.182
3	3	0.028	11,392	0.028	4	0.035
4	4	0.012	15,443	0.012	6	0.016
5	5	0.004	17,560	0.004	9	0.005
6	6	0.002	18,520	0.002	12	0.002
7	7	0.001	19,006	0.001	16	0.001
8	8	0.0002	19,605	0.0002	23	0.0003
9	9	0.0001	19,847	0.0001	28	0.0001

ronmental breadth and geographic range (Table 3).

We assessed the strength of selectivity based on normalized data in two ways. First, we determined the log odds ratio from 2×2 contingency tables that tally survival versus extinction in genera in the first quantile versus all other quantiles combined. (Because the first quantile of the distribution of species richness corresponds to genera with a single species, normalization has no effect on the 2×2 table for species.) Second, we carried out logistic regressions using geographic range, environmental breadth, and species richness in turn as predictor variables and the log odds of survival as the response variable. This was executed in R (R Development Core Team 2011) using the command `glm(Y~X, family = binomial)`, where Y denotes extinction (0) versus survival (1), and X is the normalized predictor variable. The slope of this regression, β , estimates the increase in the log odds of survival corresponding to a unit increase in the predictor variable, i.e., an increase in the value of the normalized ordered variate from n to $n+1$ (Agresti 2007: p. 71). This approach has been used extensively in recent years to study selectivity of extinction (Payne and Finnegan 2007; Finnegan et al. 2008; Wang and Bush 2008); those works can be consulted

for further detail. Because the distributions of predictor variables are normalized, the strength of various predictors can be directly compared. Results based on contingency tables are generally qualitatively similar to those based on logistic regression, and so in most cases we present only the former.

Results and Additional Analyses

All three variables have a positive effect on the probability that a genus will survive past its stage of first appearance (Tables 2, 4, Fig. 3). Geographic range has the strongest effect, followed by environmental breadth and species richness, although the difference between geographic range and environmental breadth is not so pronounced when based on logistic regression (Fig. 3B). It is surprising that, on the whole, genera in the fifth and higher quantiles, i.e., with nine or more species (Table 3), have lower survivorship than genera with fewer species (Fig. 3C), although it is worth noting that these genera account for less than 1% of the total. This odd feature is most conspicuous in Mesozoic genera (Fig. 4). We will explore temporal variation in selectivity in more detail below.

Sensitivity Analysis.—To test the robustness of these results, we carried out several variants of the basic analysis (Fig. 5):

TABLE 4. Survivorship with respect to normalized geographic range. *Restricted* refers to genera in the first quantile (Table 3); *widespread* refers to all other quantiles combined. Results for environmental breadth and species richness are the same as in Table 2.

	No. of genera not surviving to next stage	No. of genera surviving to next stage	Probability of survival	Odds of survival	Odds ratio	Log odds ratio	Standard error
Restricted	8807	9467	0.518	1.075			
Widespread	956	1995	0.676	2.087	1.941	0.663	0.0420

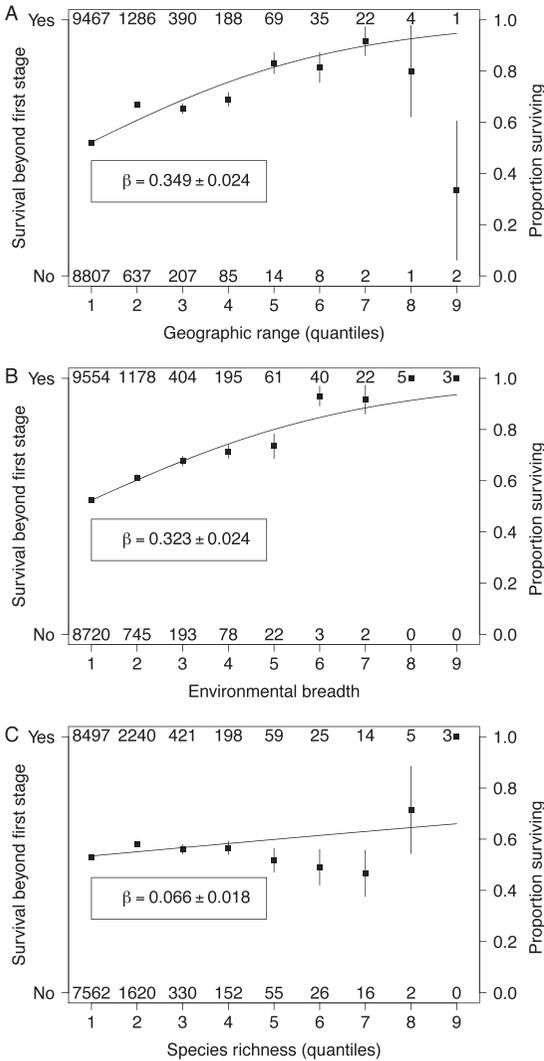


FIGURE 3. Logistic regression relating the log odds of survival past the stage of first appearance to the predictor variables geographic range (A), environmental breadth (B), and species richness (C). The last two values are normalized to have the same statistical distribution as environmental breadth (see text for details). Integers within the graph show the number of genera that do and do not survive for each value of the predictor. Solid squares show the proportion of genera surviving, plus or minus one binomial standard error. The solid line is the logistic regression; note that although this follows the trend in the solid squares, it is not fitted to those points. Inset boxes give the regression coefficient, plus or minus one standard error; this coefficient gives the expected increase in the log odds of survival with each unit increase in the predictor variable (the “incremental log odds of survival” in Fig. 5B).

1. Our protocol for assigning species richness yields an absolute minimum number of species per genus. We varied this protocol by omitting genera except those in which

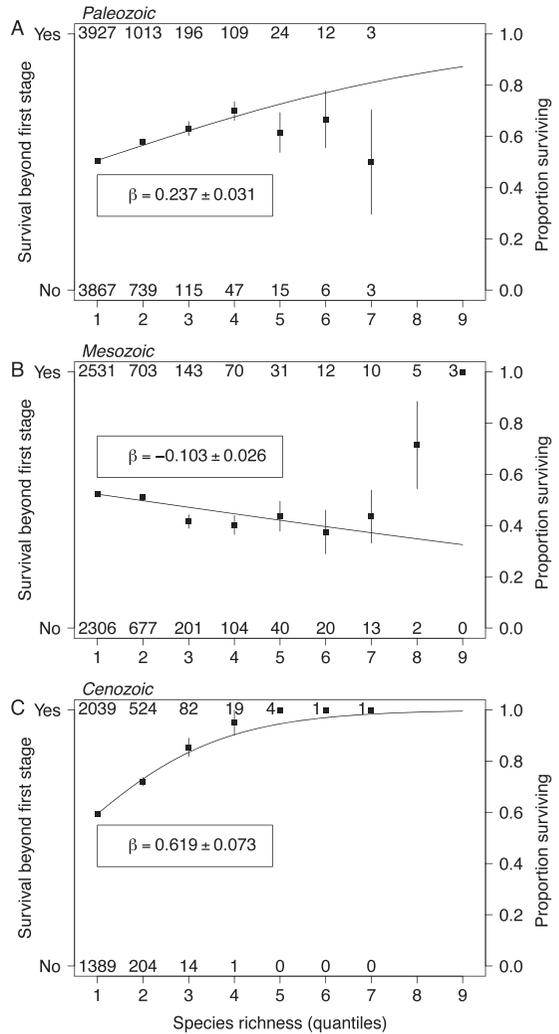


FIGURE 4. Logistic regression of survival against species richness, with separate analyses for Paleozoic, Mesozoic, and Cenozoic genera. See Figure 3 for explanation. The decrease in survivorship with increasing species richness seen in Figure 3C is mainly characteristic of Mesozoic genera.

all occurrences consist of named species. The one exception is that we retained genera known from a single “sp.” occurrence in a single collection, since it is reasonable to infer that such genera are monotypic. This variation results in a very slight reduction in apparent selectivity with respect to species richness (Fig. 5).

2. Similarly, we varied the protocol for handling unknown environments by excluding genera with any occurrences from unknown or unspecified environments. How-

Sensitivity analysis

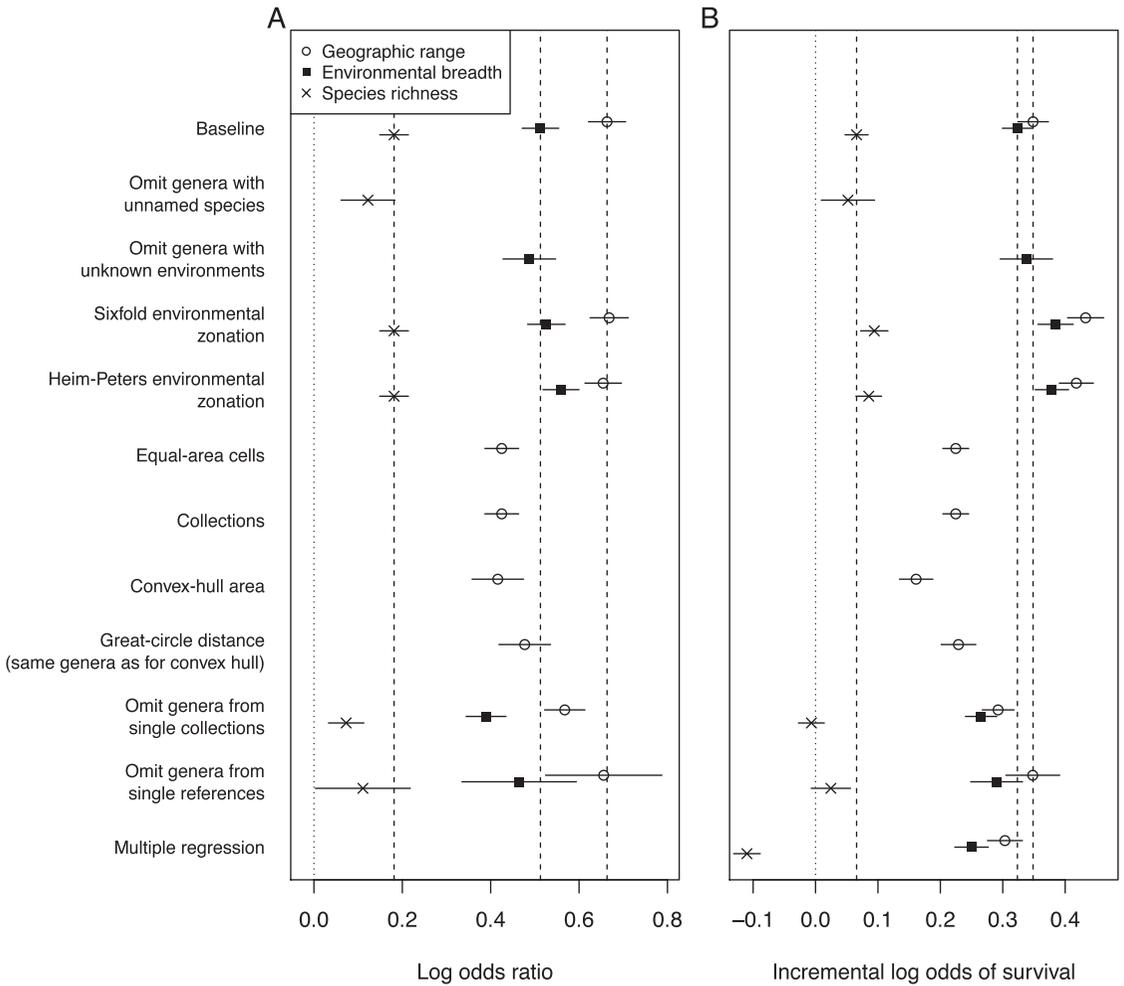


FIGURE 5. Sensitivity analyses showing how results are affected by alternative protocols for treating the data. Error bars are plus or minus one standard error. See text for further discussion.

ever, we retained genera known from a single collection, since these must be confined to a single environment. The apparent selectivity with respect to environmental breadth changes only slightly (Fig. 5).

3. We used an alternative, sixfold environmental zonation (Table A1) that, with the exception of reefs, is based mainly on an onshore-offshore transect. In addition, we renormalized the species richness and geographic range to correspond to six ordered bins. The log odds ratios based on 2×2 contingency tables barely differ

(Fig. 5A). The same is true if we use the environmental zonation of Heim and Peters (2011) (Table A1). This similarity in results arises largely because most genera are confined to a single environmental zone in any of the three assignment schemes, and selective survival is largely a matter of being in one zone versus two or more zones. The fact that the logistic regressions yield stronger effect sizes with the two alternative zonations (Fig. 5B) is all but a necessary consequence of having a predictor variable with fewer categories. If the effect over the range of values is the same,

the effect per unit increase in the normalized predictor must be larger if the predictor has a smaller range of values.

4. We used an alternative measure of geographic range, the number of equal-area cells occupied by a genus, also normalized. This measure, which does not explicitly take the distance among cells into account, shows weaker selectivity (Fig. 5), albeit still substantial and still stronger than selectivity with respect to species richness. Comparing this result with the baseline analysis, we can infer that a genus stands a lower risk of extinction if it is spread out over a greater distance than if it simply occupies a greater number of distinct areas. We see very similar results if we analyze the number of collections in which a genus is found, a quantity that correlates with several measures of geographic range (Table 1) and may also be a proxy for local abundance (e.g., Brown 1984; Blackburn et al. 2006) (Fig. 5).

We also measured geographic range as the convex hull area of all genus occurrences after projecting the paleolatitudes and -longitudes as described above. Only genera with three or more distinct coordinates could be used in this analysis, so these may represent a biased sample. Selectivity is lower than in our baseline analysis (Fig. 5), but does this reflect the measure of range itself or the subset of genera included? To assess this, we reanalyzed data on great-circle distance, using only those genera included in the convex-hull analysis. The two measures yield similar results for this subset of genera, suggesting that they capture sensitivity of survival to geographic range comparably (as would be expected from their high correlation; Table 1), and that the difference between the baseline analysis and the analysis of convex-hull area reflects the skewed sample of genera rather than the nature of the measure itself. Because selectivity is lower with this sample of genera that are known from at least three distinct localities, it seems that the difference in the chances of survival is greater when we compare genera that are maxi-

mally restricted to those that are just slightly more widespread than when we make distinctions among genera that are already relatively widespread (see also Fig. 3A).

5. Genera may be highly restricted, occurring, in the most extreme cases, in a single collection. This may reflect a true biological condition or it may reflect a bias such as a Lagerstätten effect, monographic effect, or limited systematic treatment. Although we cannot necessarily determine in any given case whether these rarest of genera are truly rare or only apparently so, we can determine the potential effect they have on our results by assuming a worst possible case and treating them all as artifacts. Excluding 10,715 genera known only from single collections in their stage of first appearance, we find that the strength of selectivity is diminished (Fig. 5), as would be expected in light of the immediately foregoing results on geographic range. At the same time, with the exception of species richness in the logistic regression analysis, we still document marked selectivity of survival. Selectivity is also maintained if, in an effort to remove monographic effects, we omit 14,472 genera known from a single reference in their stage of first appearance (Fig. 5).
6. The three variates we are using to predict survivorship are positively correlated, so it is possible in principle that simple regression of survival against single variates reflects indirect effects due to correlation (Harnik 2011). To explore this possibility, we carried out multiple logistic regression of survival as a function of range, breadth, and richness. The positive effect of species richness on survival vanishes, raising the possibility that the apparent effect of species richness simply reflects correlation with the other variates (Fig. 5B) (see also Finnegan et al. 2008).

On the whole, then, the strong effect of geographic range and environmental breadth on survival is a robust feature of the data; range may have a stronger effect than breadth or an equal effect, depending on how the data

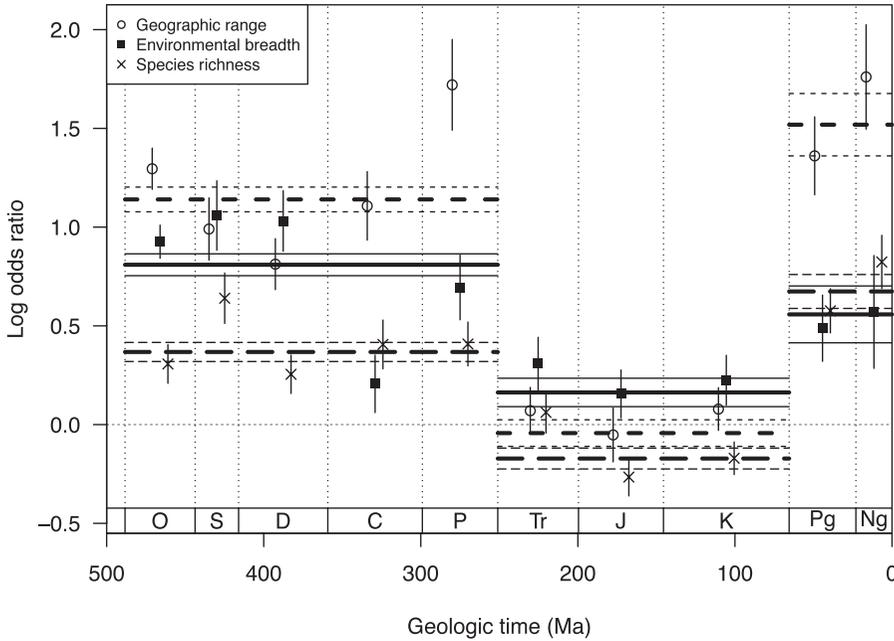


FIGURE 6. Selective survival of genera first appearing in a stage, aggregated by period (points) and by era (horizontal lines). Error bars on points and envelopes around lines represent plus or minus one standard error. Open circles and short-dashed lines, geographic range; closed squares and solid lines, environmental breadth; \times 's and long-dashed lines, species richness. Note that selectivity is weak to absent during the Mesozoic.

are treated. Species richness has the weakest effect, in fact diminishing to nil in some analyses.

Temporal and Taxonomic Variation in Selectivity.—So far we have focused on broad patterns of selectivity over nearly the entire span of the Phanerozoic. But these may mask substantial temporal variation in selectivity, which is depicted in Figure 6. The data are still analyzed at the stage level—i.e., we are still asking whether a genus endures past its stage of first appearance—but all genera originating within an entire period are aggregated into a single analysis. Superimposed are aggregate results for entire eras as well. Perhaps the most striking feature here is low selectivity of survival during the Mesozoic era. Environmental breadth does contribute to survival, but weakly compared with other intervals of time, whereas geographic range and species richness have barely any effect on the whole. We see the same result within higher taxa; those classes that are diverse enough to be analyzed separately by era (Anthozoa, Bivalvia, Cephalopoda, and Gastropoda) all show relatively low selectivity during the Mesozoic

(Fig. 7). At the same time, some gross patterns of selectivity may be highly influenced by the patterns inherent in a small number of diverse clades. This seems like a potential problem a priori, because patterns of selectivity differ systematically among higher taxa, although this among-clade variation is partly confounded by temporal variation (Wang and Bush 2008). As an example of the joint effects of taxon and time, gastropods on the whole show weaker selectivity with respect to environmental breadth than species richness or geographic range, but this arises in large part because that is the pattern they exhibit during the Cenozoic, when they are most diverse (Fig. 7).

Because higher taxa vary in their characteristic extinction rates (Stanley 1979; Wang and Bush 2008), we would expect taxonomic variation in the proportion of genera that survive past their stage of first appearance. This does not necessarily mean, however, that characteristic extinction rates influence the strength of selectivity. To explore this question, we tabulated, for each of 21 classes having at least 100 genera, the mean genus duration (an

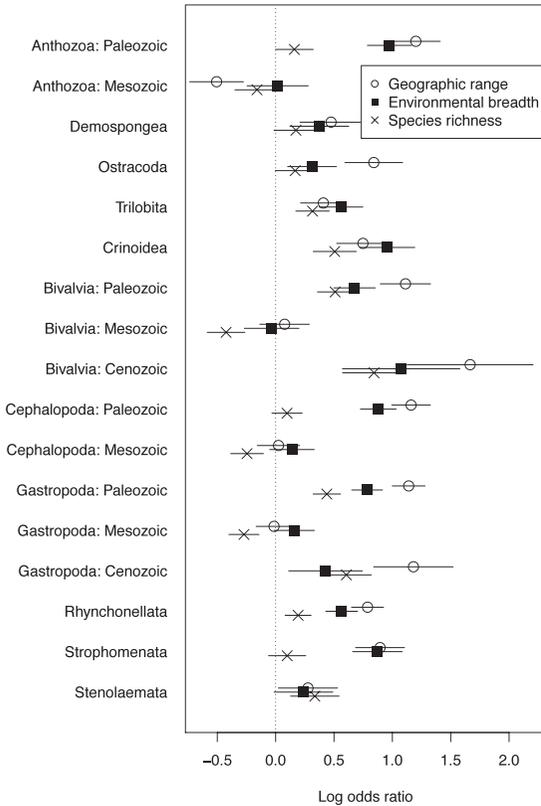


FIGURE 7. Selectivity of survival within the most diverse classes. Error bars are plus or minus one standard error. Note the generally lower selectivity in the Mesozoic, in agreement with the trend in the data at large.

inverse measure of average extinction rate) and the strength of selectivity. We find that genus duration is not a strong predictor of selectivity. For geographic range, environmental breadth, and species richness, respectively, $r_s = 0.10$ ($p = 0.66$), $r_s = -0.09$ ($p = 0.70$), and $r_s = 0.15$ ($p = 0.51$). We measured genus duration in stages, but we find similar results (not presented) if we measure duration in millions of years between the start of the stage of first appearance and the end of the stage of last appearance.

At first glance the Mesozoic results may seem inconsistent with those of Payne and Finnegan (2007), who found selectivity with respect to geographic range throughout the Phanerozoic. Operationally, there are many differences between their analysis and ours. For example, the Paleobiology Database has grown to include nearly twice as many

occurrences as when they did their study, and they measured geographic range as the number of distinct tectonic plates on which a genus occurs. They also used coarser time intervals, so that a genus has the potential to expand and diversify more within its interval of first appearance. We think none of these differences adequately explain the difference in our results, however. In analyses presented in Appendix 2, we find (1) that we can essentially replicate Payne and Finnegan's result of selectivity throughout the Phanerozoic when we use their methods and stratigraphic resolution on the newer data set (Fig. A1); (2) that selectivity in the Mesozoic is not systematically higher than in our earlier results when we use our analytical protocol but measure geographic range as number of plates (Fig. A2); and (3) that survival beyond the interval of first appearance is still largely nonselective in the Mesozoic, even when we use coarser temporal resolution (Fig. A3).

A more salient possibility is that we are restricting our analysis of selectivity to the stage of first appearance of a cohort of genera. It is conceivable that one stage is not always long enough for genera to differentiate sufficiently from each other in geographic range and other factors for these to make a difference to their relative prospects of survival. To explore this possibility, we separately analyzed genera first appearing in a stage and genera carrying over from earlier stages (Fig. 8). When we focus on genera that have had a chance to spread and diversify (see Fig. 11), we see that range, breadth, and richness have a substantial impact on survival during most time intervals, basically consistent with what Payne and Finnegan (2007) found.

Why is selective survival of young genera so weak, if not altogether absent, during the Mesozoic? One possibility is that Mesozoic genera are relatively undifferentiated from each other in the factors that affect early survival. However, differentiation among genera in range, breadth, and richness is generally at least as high during the Mesozoic as it is at most other times (Fig. 9). If we inspect the shapes of the distributions by stage (analogous to Fig. 1), we see that variance on the whole is strongly and inversely correlated

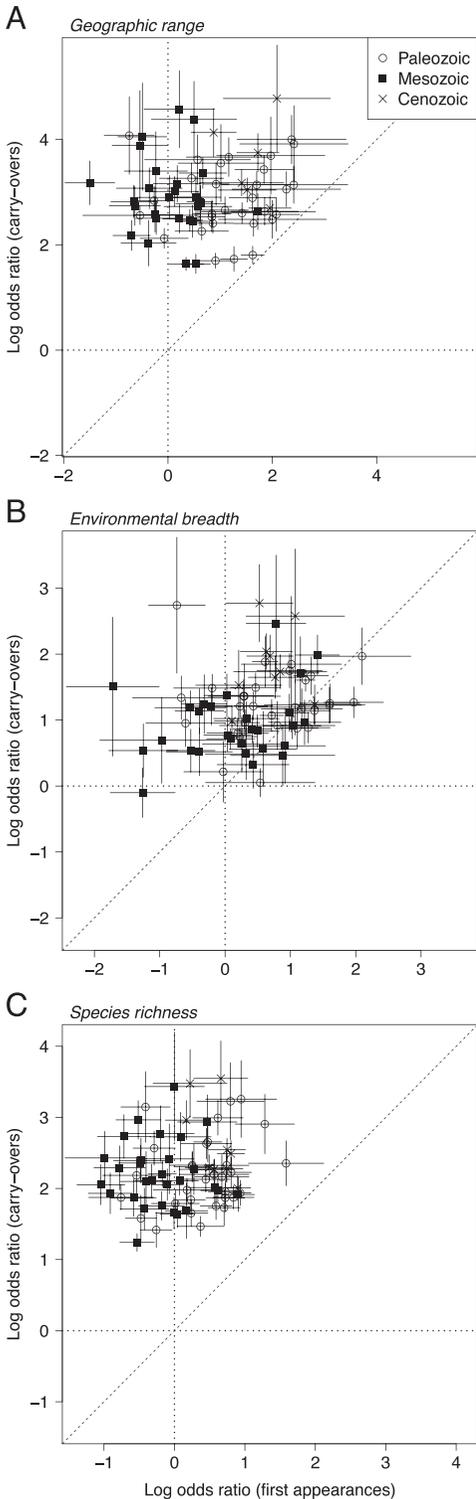


FIGURE 8. Selective survival analyzed stage by stage for genera first appearing in a stage (abscissa) and genera carrying over from prior stages (ordinate). Points and error bars as in Figure 6. Diagonal dashed line is the 1:1

with the frequency of genera with the lowest possible value of a given variate (results not presented), which stands to reason in light of the extreme skewness of these distributions. So, for example, the stages with higher variance in species richness are also those with the lower frequency of monotypic genera. The high variance in the Mesozoic may suggest some connection to low selectivity, but we offer two reasons to think this is not the case. First, the result goes against the prior expectation that greater differentiation should allow greater selectivity, a result that is supported when we look at how selectivity and differentiation increase with genus age (see next section). Second, if we compare the variance among genera first appearing in each stage with the strength of selectivity of survival to the next stage, detrended by taking first differences, we find essentially no correlation; for range, breadth, and richness, respectively, $r_s = -0.03$ ($p = 0.82$), $r_s = -0.12$ ($p = 0.32$), and $r_s = -0.07$ ($p = 0.58$). Selectivity can also be diminished if survivorship is unusually high or low. However, the proportion of genera that survive past their stage of first appearance is not very different during the Mesozoic compared with other times (Fig. 2).

Stage length could in principle contribute to lower selectivity in the Mesozoic, because shorter stages mean less time for genera to differentiate from one another. On the whole, there is a positive, albeit not generally strong, association between stage length and both the variance among genera first appearing in the stage (range: $r_s = 0.37$, $p = 0.002$; breadth: $r_s = 0.20$, $p = 0.097$; richness: $r_s = 0.11$, $p = 0.36$) and the strength of selectivity (range: $r_s = 0.19$, $p = 0.12$; breadth: $r_s = 0.32$, $p = 0.007$; richness: $r_s = 0.17$, $p = 0.16$). However, this effect does not appear to be sufficient to account for overall low selectivity in the Mesozoic. First, the difference in average stage length among eras is comparatively small (7.7 Myr for the

line. Note the stronger selectivity when established genera, which have had time to expand and diversify, are included.

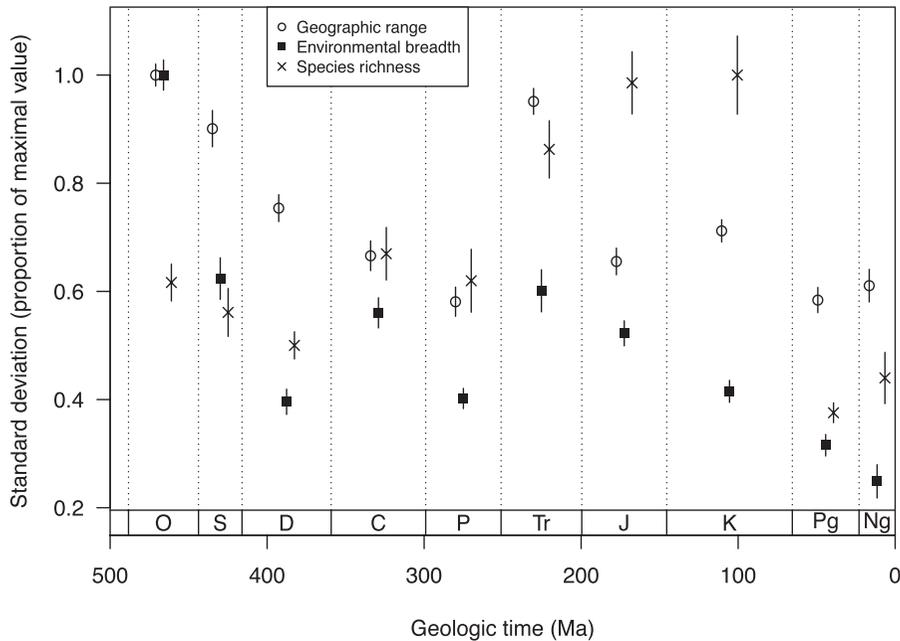


FIGURE 9. Differentiation of range, breadth, and richness among genera first appearing in a stage, based on raw (i.e., not normalized) data. Genera are grouped by period. To allow all data to be plotted on the same scale, standard deviations for each property are scaled relative to the maximum value for each respective time series. Error bars are plus or minus one standard error, based on bootstrap resampling. Times of low selectivity (Fig. 6) do not generally correspond to times of low differentiation among genera.

Paleozoic, 6.4 for the Mesozoic, and 6.7 for the Cenozoic [Ogg et al. 2008]). Second, even if we control for stage length, the Mesozoic still stands out for lower selectivity. This is most easily seen graphically (Fig. 10); even at shorter than average stage lengths, Paleozoic and Cenozoic stages generally stand out above those of the Mesozoic. This contrast is strongest for geographic range and least distinct for environmental breadth. We can also demonstrate the contrast statistically with analysis of variance to measure the effects of stage length and era (Paleozoic plus Cenozoic versus Mesozoic) on the log odds ratio (Table 5). For geographic range and species richness, era has a much stronger effect than stage length. For environmental breadth, stage length and era have effects of comparable magnitude.

For the moment we must regard low selectivity in the Mesozoic as an unexpected and unexplained phenomenon, but a real phenomenon.

Effects of Genus Age.—As genera age, they have the potential to differentiate from one

another in properties such as geographic range. As expected, the variance among genera in geographic range and other properties increases with genus age (Fig. 11A), the effect being strongest in the transition from the first to the second stage. Although it is not a logical necessity that such an increase in variance must lead to an increase in selectivity, this is in fact what we observe (Fig. 11B); differences in geographic range, environmental breadth, and species richness become more important in determining which genera survive further. Note that this is not a matter of selectivity of extinction with respect to genus age (Finnegan et al. 2008), but rather of how selectivity with respect to other properties itself depends on genus age. Moreover, it suggests that models that explore the effects on survival of genus age and other factors such as geographic range should incorporate interaction terms between age and other factors, rather than assuming additive effects (Finnegan et al. 2008). Because selectivity with respect to range and other traits is stronger for older genera, it is possible, in a purely additive

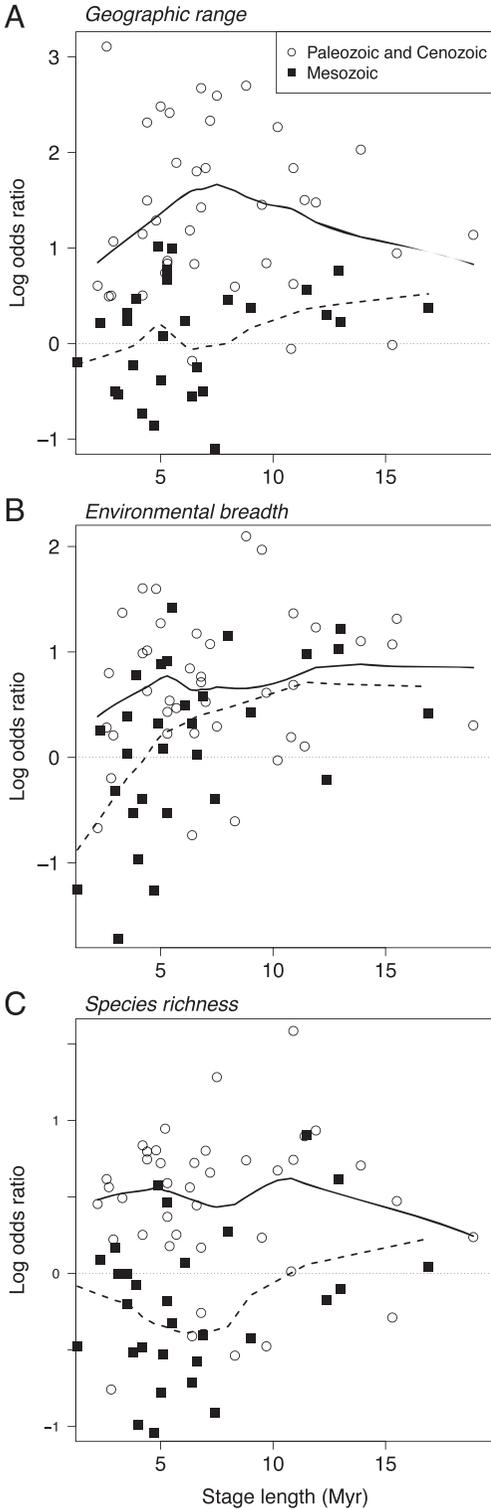


FIGURE 10. Comparison of stage length and strength of selectivity. Each point represents a stage; lines show lowess regressions through the combined Paleozoic and Cenozoic (solid) and Mesozoic (dashed) stages, using a

model, that this could be expressed statistically as an effect of genus age on the odds of survival.

Discussion and Conclusions

How sampling should effect the apparent strength of selectivity is not straightforward. For example, with less-complete sampling, there will generally be a greater offset between the true time of origination and the time of first appearance, which might lead one to expect genera to appear initially with a wider geographic range (Fig. 11). At the same time, this range might be biased downward by incomplete sampling, because there will be fewer localities sampled in any interval of time. Also, with less-complete sampling, there will be a greater offset between the true time of extinction and the time of last appearance, so the proportion of genera surviving past their stage of first appearance will be biased downward. To explore the effects of these interacting biases, we conducted a simple simulation. We started with the raw data analyzed herein as if they were complete. This has certain advantages over completely fabricating an artificial data set. For example, a spectrum of rare and common genera, with varying chances of being sampled, is maintained. We then degraded the data by randomly removing collections and tabulated all relevant quantities—stratigraphic range, geographic range, and so on—based on the degraded data (Fig. 12). For simplicity, we present results only for geographic range. We find that the mean range and differentiation among genera increase as sampling increases (Fig. 12B), and that, as expected, apparent survival beyond the stage of first appearance increases with the completeness of sampling (Fig. 12C). Because geographic range increases more slowly than apparent survival, however, the effect of sampling on the strength of selectivity is not monotonic (Fig. 12D). Selectivity is generally biased downward by

←
smoothing span of 0.67. Although there is generally a weak positive relationship, this does not adequately explain low selectivity in the Mesozoic (see also Table 5).

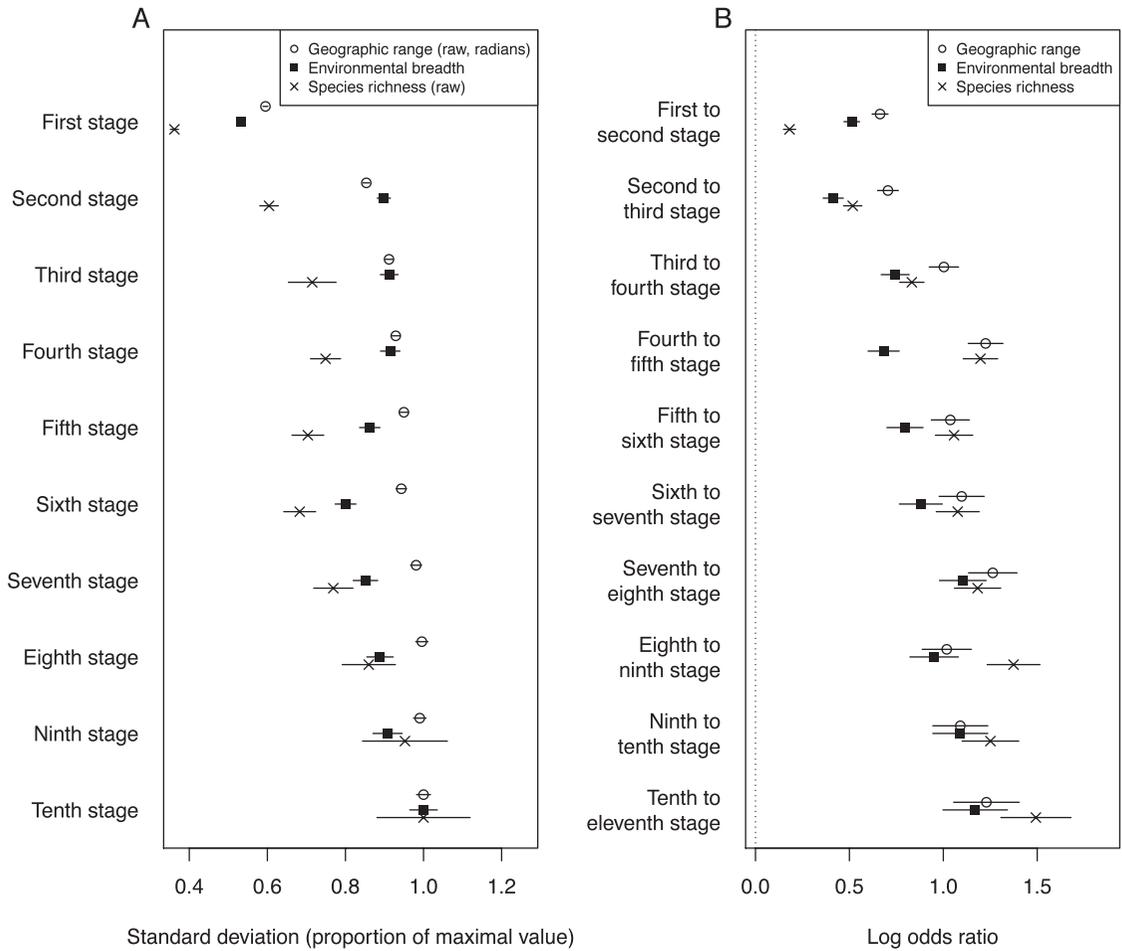


FIGURE 11. Effects of genus age. A, Standard deviation of genus properties increases with age; error bars as in Figure 9. B, The effect of range, breadth, and richness on survival to the next stage also increases, as genera differentiate more in these properties.

incomplete sampling, but there is substantial selectivity at all levels of sampling. This suggests that the presence of selectivity in our data is unlikely to be a mere sampling

artifact. Given that the effect of sampling on apparent selectivity is much less than the observed temporal variation in selectivity (Fig. 6), and that it does not seem possible to

TABLE 5. Analysis of variance showing effect of stage length and era (Paleozoic plus Cenozoic versus Mesozoic) on the log odds ratio.

Genus property	Source of variation	df*	Sum of squares	Mean square	F	p
Geographic range	Stage length	1	0.78	0.78	1.4	0.24
	Era	1	26.6	26.6	48.0	<0.001
	Residuals	64	34.9	0.55		
Environmental breadth	Stage length	1	3.95	3.95	8.0	0.0062
	Era	1	3.85	3.85	7.8	0.0067
	Residuals	65	32.0	0.49		
Species richness	Stage length	1	0.70	0.70	2.9	0.092
	Era	1	6.55	6.55	27.2	<0.001
	Residuals	66	15.6	0.24		

* Degrees of freedom vary among analyses because not all stages can be included in every analysis. The log odds ratio for geographic range is infinite in two stages (Aalenian and upper Eocene), because there are no genera that are widespread and fail to survive to the next stage. Likewise, for environmental breadth in one stage (Moscovian), there are no genera that are broad and fail to survive.

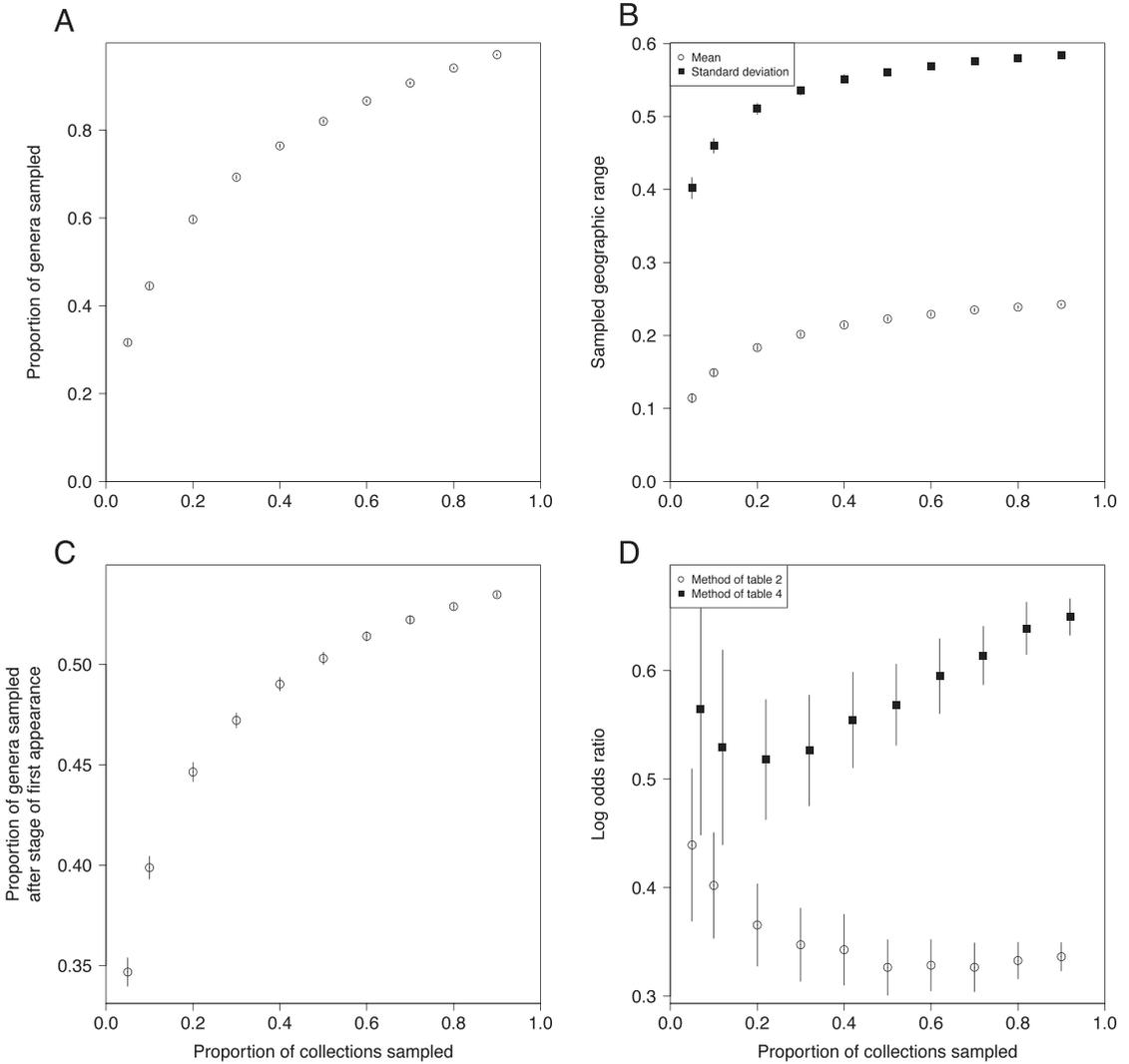


FIGURE 12. Simulation of effects of incomplete sampling. Each point shows the mean of 100 simulations; error bars show plus or minus one standard error. Sampled proportions are 0.05 and 0.1 through 0.9 in increments of 0.1; points in D are plotted offset for clarity. In each simulation, a proportion of collections is randomly omitted and the stratigraphic and geographic ranges of genera are tabulated based on the degraded data. The proportion of genera sampled (A), the mean and standard deviation of geographic range (B), and the proportion of genera found after their stage of first appearance (C) increase with the completeness of sampling. The strength of selectivity is affected less, however (D). This suggests that selectivity itself, as well as substantial temporal variation in selectivity (Fig. 6), is not an artifact of incomplete sampling.

degrade data sufficiently to remove apparent selectivity (Fig. 12D), it also seems unlikely that temporal variation in the quality of sampling can explain features such as unusually low selectivity during the Mesozoic.

We have attempted to make geographic range, environmental breadth, and species richness comparable analytically by normalizing the data. There is, however, one way in

which they may not be comparable, namely in the degree of certainty with which each quantity is known. If all three properties were equally important predictors of survival, but if, as seems at least plausible, geographic range were known with greater certainty, then environmental breadth and species richness could appear to be less important selective agents. The relative importance of these three

factors therefore must be viewed with some caution. However, the fact that the differences among these factors diminish as genera age (Fig. 11) suggests that such differences are not somehow forced by our data and methods. We will therefore accept them at face value for the sake of discussion.

We have found that genera that expand more rapidly early in their history are more likely to survive past their inception. This leaves open the question of why some taxa expand more rapidly than others. Liow et al. (2010) tested whether microfossil species that experience greater initial environmental volatility tend to be the ones that expand more rapidly and found the answer to be negative. Our approach here has been mainly exploratory, to determine whether there are conspicuous differences among factors that predict early survival of genera and temporal trends in selectivity. Given the premise that a genus diversifies its portfolio and reduces risk by having more species and being more widespread environmentally and geographically, we are not surprised to find that those genera that get off to a faster start in these respects are more likely to survive. Our results nonetheless raise some interesting questions that deserve further attention:

1. In terms of early survival, species richness is generally the least important of the factors we have considered. This is evidently a feature peculiar to young genera, for, as genera age, richness, geographic range, and environmental breadth all increase and become roughly equally important in reducing extinction risk (see also Finnegan et al. 2008). It takes genera less time to achieve enough of a geographic and environmental spread to make a difference than it does for them to diversify enough to make a difference.
2. During much of the Mesozoic, neither geographic range nor species richness is very effective in promoting the early survival of new genera. This puzzling result does not arise because genera fail to expand and diversify, however, as there is considerable differentiation among them (Fig. 9). Nor does it seem likely that range

and richness simply do not matter in general during this span of time, because they do enhance survival of more established genera during the Mesozoic (Fig. 8) (Payne and Finnegan 2007). Nor are we inclined to throw up our hands and blame bad data or some unspecified bias, because we know the data we have analyzed are capable of detecting selective survival for established genera. Rather, some factors we have failed to take into account, possibly organismal traits such as body size, life habit or trophic mode (McKinney 1997; Payne 2005; Crampton et al. 2010; Harnik 2011), or demographic traits such as abundance and patchiness of distribution (McKinney 1997; Lockwood 2003; Jablonski 2008; Harnik 2011; Harnik et al. 2012) may explain which genera survive past their inception and which do not. In any event, there appears to be a considerable stochastic element to the early survival of Mesozoic genera.

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Appendix 1

Assignment of Paleoenvironments

TABLE A1. Assignment of environments to environmental zones.

Environment	Environmental zone (elevenfold division)	Environmental zone (sixfold division)	Heim and Peters zones
Lagoonal/restricted shallow subtidal	Marginal marine (carbonate)	Marginal marine	Nearshore
Peritidal	Marginal marine (carbonate)	Marginal marine	Peritidal
Delta plain	Marginal marine (clastic)	Marginal marine	Peritidal
Estuary/bay	Marginal marine (clastic)	Marginal marine	Peritidal
Interdistributary bay	Marginal marine (clastic)	Marginal marine	Nearshore
Lagoonal	Marginal marine (clastic)	Marginal marine	Nearshore
Marginal marine indet.	Marginal marine (clastic)	Marginal marine	Peritidal
Paralic indet.	Marginal marine (clastic)	Marginal marine	Peritidal
Open shallow subtidal	Shallow subtidal (carbonate)	Shallow subtidal	Shallow shelf
Sand shoal	Shallow subtidal (carbonate)	Shallow subtidal	Offshore shoal
Shallow subtidal indet.	Shallow subtidal (carbonate)	Shallow subtidal	Peritidal
Delta front	Shallow subtidal (clastic)	Shallow subtidal	Offshore shoal
Foreshore	Shallow subtidal (clastic)	Shallow subtidal	Peritidal
Shoreface	Shallow subtidal (clastic)	Shallow subtidal	Peritidal
Deep subtidal ramp	Deep subtidal (carbonate)	Deep subtidal	Deep shelf
Deep subtidal shelf	Deep subtidal (carbonate)	Deep subtidal	Deep shelf
Deep subtidal indet.	Deep subtidal (carbonate)	Deep subtidal	Slope and basin
Transition zone/lower shoreface	Deep subtidal (clastic)	Deep subtidal	Shallow shelf
Offshore ramp	Offshore (carbonate)	Offshore	Deep shelf
Offshore shelf	Offshore (carbonate)	Offshore	Deep shelf
Offshore indet.	Offshore (carbonate)	Offshore	Slope and basin
Offshore	Offshore (clastic)	Offshore	Deep shelf
Prodelta	Offshore (clastic)	Offshore	Shallow shelf
Slope	Carbonate slope	Slope and basin	Slope and basin
Basinal (carbonate)	Slope and basin	Slope and basin	Slope and basin
Basinal (siliciclastic)	Slope and basin	Slope and basin	Slope and basin
Basinal (siliceous)	Slope and basin	Slope and basin	Slope and basin
Deep-water indet.	Slope and basin	Slope and basin	Slope and basin
Submarine fan	Slope and basin	Slope and basin	Slope and basin
Reef, buildup, or bioherm	Reef	Reef	Reef
Perireef or subreef	Reef	Reef	Reef
Intrashelf/intraplatform reef	Reef	Reef	Reef
Platform/shelf-margin reef	Reef	Reef	Reef
Slope/ramp reef	Reef	Reef	Reef
Basin reef	Reef	Reef	Slope and basin
Carbonate indet.	Unknown	Unknown	Unknown
Coastal indet.	Unknown	Unknown	Peritidal
Deltaic indet.	Unknown	Unknown	Shallow shelf
Marine indet.	Unknown	Unknown	Unknown

TABLE A2. Cross-tabulation of environment by primary lithology. All downloaded collections are included.

Environment	No. of collections	Proportion carbonate	Proportion clastic	Proportion mixed	Proportion other or unknown
Lagoonal/restricted shallow subtidal	922	0.828	0.097	0.069	0.007
Peritidal	216	0.764	0.167	0.060	0.009
Delta plain	23	0.043	0.957	0.000	0.000
Estuary/bay	380	0.039	0.889	0.037	0.034
Interdistributary bay	48	0.000	1.000	0.000	0.000
Lagoonal	202	0.208	0.673	0.079	0.040
Marginal marine indet.	516	0.062	0.837	0.031	0.070
Paralic indet.	47	0.000	0.957	0.000	0.043
Open shallow subtidal	2630	0.766	0.070	0.102	0.062
Sand shoal	117	0.949	0.043	0.000	0.009
Shallow subtidal indet.	5413	0.821	0.107	0.048	0.024
Delta front	170	0.071	0.918	0.012	0.000
Foreshore	258	0.116	0.748	0.008	0.128
Shoreface	561	0.078	0.816	0.057	0.048
Deep subtidal ramp	619	0.858	0.116	0.019	0.006
Deep subtidal shelf	1115	0.641	0.270	0.078	0.011
Deep subtidal indet.	844	0.652	0.126	0.210	0.013
Transition zone/lower shoreface	1640	0.106	0.861	0.019	0.014
Offshore ramp	725	0.782	0.161	0.052	0.004
Offshore shelf	1219	0.564	0.287	0.142	0.007
Offshore indet.	793	0.694	0.129	0.098	0.079
Offshore	4791	0.070	0.872	0.034	0.024
Prodelta	416	0.002	0.969	0.029	0.000
Slope	1219	0.925	0.067	0.006	0.002
Basinal (carbonate)	897	0.637	0.115	0.245	0.003
Basinal (siliciclastic)	360	0.007	0.896	0.014	0.083
Basinal (siliceous)	144	0.122	0.636	0.239	0.003
Deep-water indet.	836	0.262	0.711	0.012	0.016
Submarine fan	154	0.266	0.714	0.006	0.013
Reef, buildup, or bioherm	5005	0.957	0.022	0.008	0.013
Perireef or subreef	731	0.896	0.056	0.038	0.010
Intrashelf/intraplatform reef	53	0.377	0.000	0.000	0.623
Platform/shelf-margin reef	61	0.951	0.033	0.000	0.016
Slope/ramp reef	51	0.961	0.020	0.020	0.000
Basin reef	12	0.833	0.167	0.000	0.000
Carbonate indet.	7045	0.880	0.056	0.037	0.026
Coastal indet.	5556	0.032	0.861	0.038	0.069
Deltaic indet.	137	0.022	0.956	0.007	0.015
Marine indet.	24,918	0.204	0.486	0.040	0.270
None given	2833	0.419	0.285	0.046	0.250

Appendix 2

Further Analyses of Selectivity with Respect to Geographic Range

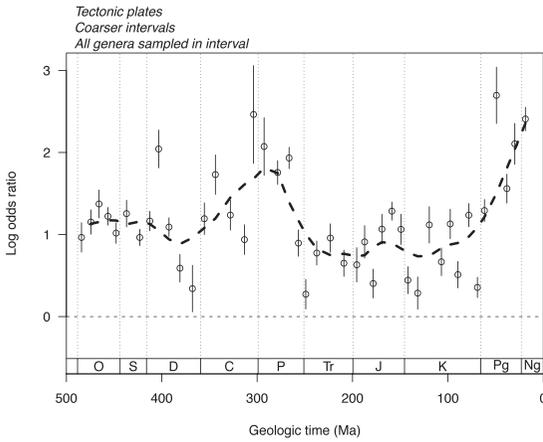


FIGURE A1. Selectivity of survival with respect to geographic range, measured as the number of distinct tectonic plates on which a genus is found. To attempt to replicate the results of Payne and Finnegan (2007), all genera sampled in each time interval are included, and coarser time intervals, the so-called 11-million-year bins of the Paleobiology Database, are used. As did Payne and Finnegan, we find selectivity throughout the Phanerozoic.

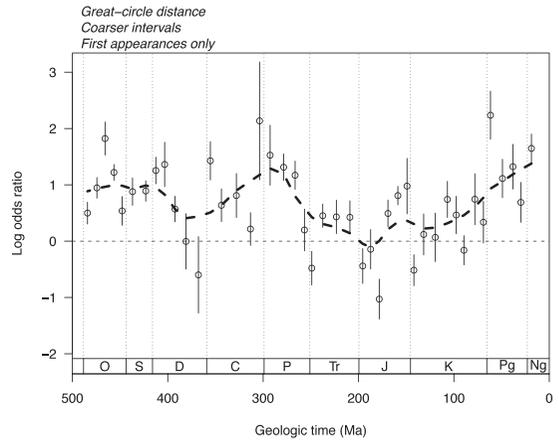


FIGURE A3. Selectivity of survival with respect to geographic range, measured as the maximum great-circle distance between localities containing a genus (see Fig. 6). Using coarser “11-million-year” bins and genera first appearing in a stage, we still find weak selectivity during much of the Mesozoic. Therefore the weak selectivity detected with stage-level data (Fig. 6) does not seem to be a simple consequence of the use of these finer time intervals.

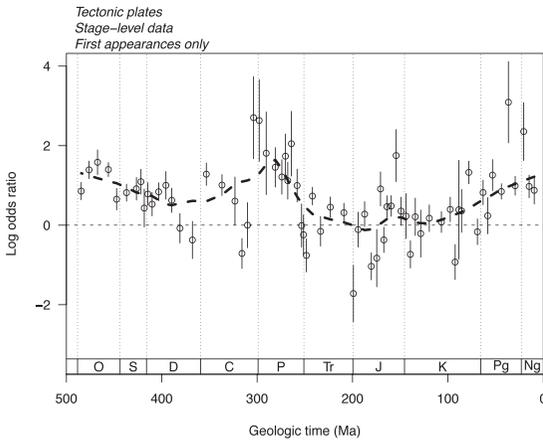


FIGURE A2. Selectivity of survival with respect to geographic range, measured as the number of distinct tectonic plates on which a genus is found. Using stage-level data and confining our analysis to genera first appearing in a stage, we find weak selectivity during much of the Mesozoic. Therefore the weak selectivity detected with great-circle distance as a measure of geographic range (Fig. 6) does not seem to be a simple consequence of the choice of range measure.