The effect of geographic range on extinction risk during background and mass extinction

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Wide geographic range is generally thought to buffer taxa against extinction, but the strength of this effect has not been investigated for the great majority of the fossil record. Although the majority of genus extinctions have occurred between major mass extinctions, little is known about extinction selectivity regimes during these ''background'' intervals. Consequently, the question of whether selectivity regimes differ between background and mass extinctions is largely unresolved. Using logistic regression, we evaluated the selectivity of genus survivorship with respect to geographic range by using a global database of fossil benthic marine invertebrates spanning the Cambrian through the Neogene periods, an interval of ≈500 My. Our results show that wide geographic range has been significantly and positively associated with survivorship for the great majority of Phanerozoic time. Moreover, the significant association between geographic range and survivorship remains after controlling for differences in species richness and abundance among genera. However, mass extinctions and several second-order extinction events exhibit less geographic range selectivity than predicted by range alone. Widespread environmental disturbance can explain the reduced association between geographic range and extinction risk by simultaneously affecting genera with similar ecological and physiological characteristics on global scales. Although factors other than geographic range have certainly affected extinction risk during many intervals, geographic range is likely the most consistently significant predictor of extinction risk in the marine fossil record.

invertebrate | Phanerozoic | selectivity | survivorship

Nearly all species that have existed on Earth are now extinct, but the precise cause of extinction for most individual species is unknown and likely unknowable. Across many taxa, however, selectivity of survivorship can shed light on extinction mechanisms. Therefore, fossil data have the potential to shed light on the factors that have been associated with extinction risk through the history of life and may even aid in assessing extinction risk for living species.

Variation in extinction intensity through the Phanerozoic suggests the primary causes of extinction may differ among intervals, a hypothesis supported by similar variation in geological and geochemical signatures among extinction events. Three mass extinctions are clearly identifiable as outliers relative to surrounding intervals (1), but geological evidence suggests that widespread environmental disturbances were associated with increases in extinction intensity during many other intervals, even if not statistically distinguishable from background at the temporal resolution currently available (2, 3). Nevertheless, most genus extinctions (≈80%) have occurred during the intervals between major mass extinctions. These background intervals are comparatively less studied, and little is known about the extinction selectivity patterns associated with them. Consequently, there has been continuing debate about whether the differences in cause and consequence between background and mass extinctions are qualitative or merely quantitative (1, 4–6).

Although geographic range is perhaps the most widely cited determinant of extinction risk for both extant and fossil taxa (7–12), the selectivity of extinction with respect to geographic range has been evaluated for only a handful of higher taxa and extinction events in the fossil record (9). Because many proposed extinction mechanisms predict particular patterns of extinction selectivity with respect to range and other variables, a systematic comparison of selectivity regimes during background and mass extinctions can help illuminate the degree to which they may represent fundamentally distinct processes.

In this study, we use benthic marine invertebrate fossil occurrences in the Paleobiology Database (PBDB), a global database of fossil occurrences, to test the association between geographic range and survivorship over an interval of ≈500 My. We find that geographic range is a strong and consistent predictor of extinction risk in the marine fossil record, but that geographic range selectivity is weakest in association with mass extinction even after accounting for extinction intensity. We suggest that widespread environmental disturbance weakens the association between geographic range and extinction risk by simultaneously affecting genera with similar ecological and physiological characteristics on global scales.

Results

The dataset analyzed contains 227,229 occurrences of 12,300 benthic marine invertebrate genera from the Middle Cambrian through the Middle Miocene, with occurrences subdivided into geological intervals of ≈10 My. We evaluated the association between geographic range and extinction rate by using logistic regression, rather than standard linear regression, because the outcome (extinction versus survival) is binary rather than continuous. In logistic regression, the odds ratio is a measure of the relationship between the odds of an outcome and an explanatory variable, in this case, the odds of survival [$p/(1 - p)$, where p is the probability of survival] and geographic range. The odds ratio is thus analogous to the slope in a standard linear regression, and its statistical significance can be easily evaluated (see *Data and Methods* for further details). Throughout this paper, we present the natural logarithm of the odds ratio (log-odds). Log-odds of zero indicate no association between the outcome and explanatory variable, just as a slope of zero indicates an absence of association in standard linear regression. Log-odds significantly greater or less than zero indicate positive and inverse associations between outcome and explanatory variable, respectively.

Geographic range has been positively associated with survivorship throughout the fossil record (Fig. 1*A*), significantly so in 44 of 47 time intervals examined [Fig. 1*A* and supporting information (SI) Table 2]. To further evaluate the causal importance of this result, we performed multiple logistic regression to estimate the

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Abbreviations: PBDB, Paleobiology Database; P–T, Permian–Triassic; T–J, Triassic–Jurassic; K–T, Cretaceous–Paleogene.

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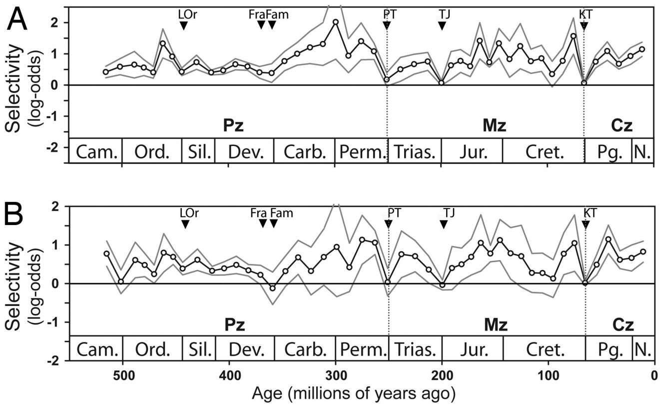

Fig. 1. Phanerozoic trends in the geographic range selectivity of genus survivorship. Log-odds of zero indicate no association, positive log-odds indicate a positive association between geographic range and extinction risk, and negative log-odds indicate an inverse association. Note that selectivity is least pronounced at times of major extinction events (indicated with arrows) but generally indicates a positive and significant association between geographic range and survivorship. (*A*) Selectivity estimated from a single logistic regression of geographic range versus survivorship. (*B*) Geographic range selectivity from multiple logistic regression of geographic range, species richness, and occurrence frequency versus survivorship. Gray lines are 95% confidence intervals on estimated odds ratios. Logarithmic vertical axes are used to preserve symmetry. Pz, Paleozoic; Mz, Mesozoic; Cz, Cenozoic; Cam., Cambrian; Ord., Ordovician; Sil., Silurian; Dev., Devonian; Carb., Carboniferous; Perm., Permian; Trias., Triassic; Jur., Jurassic; Cret., Cretaceous; Pg., Paleogene; N., Neogene. Major extinction events are indicated by arrows: LOr, Late Ordovician; Fra, Frasnian; Fam, Fammenian; PT, P–T; TJ, T–J; KT, K–T. Estimates are less stable in the multiple regression (i.e., 95% confidence intervals are broader) because the three examined variables are collinear.

effect of geographic range on genus survivorship independent of two potentially confounding variables: species richness and number of global occurrences. The pattern of geographic range selectivity obtained from multiple regression is not substantially different from that obtained from single regression (Fig. 1*B* and SI Table 3). Thus, although species richness and occurrence frequency are each strongly associated with survivorship when analyzed individually (SI Table 4), geographic range selectivity in our data set is not merely a consequence of correlation with these other genus attributes. In fact, geographic range is more consistently associated with extinction risk than are the other two variables (SI Tables 3 and 5), suggesting that associations of richness and occurrence frequency with extinction risk in single regressions partly reflect correlation with geographic range.

Incompleteness and heterogeneity of the fossil record and related databases can have substantial effects on observed fossil diversity (13, 14). However, we must emphasize that the consequences of this incompleteness for analyzing extinction selectivity are different, and generally less severe, than for analyses depending on absolute measures of diversity or geographic range. Although genera in well sampled intervals will clearly tend to exhibit larger absolute ranges than genera in poorly sampled intervals, the goal of our study is not to estimate changes in geographic range through time but, rather, to examine the differential extinction risk associated with varying range size among all genera within each interval. By asking whether widespread or narrowly distributed genera are preferentially likely to go extinct within each interval, we assume only that the observed differences in geographic range reflect actual differences, however imperfectly. To affect the results of this study, there would need to be a tendency within time intervals for the observed geographic ranges of victims to differ from those of survivors independent of their actual geographic ranges, occurrence frequencies, and species richness. We are unaware of any reasonable model of sampling bias that would produce such a distortion.

Table 1. Correlations between geographic range selectivity and change in metrics of record quality

Factor	*N*	Slope	R^2	*P*
Occurrences in PBDB	46	−0.276	0.021	0.334
Tectonic plates in PBDB	46	0.067	0.203*	**0.002**
Named geological formations (USA)†	46	0.004	0.018	0.369
Global sea level‡	46	−0.005	0.029	0.255
Percent of diversity represented by range-through genera	46	−2.738	0.069	0.077

Results are presented for comparisons of interval-to-interval changes in record quality (first differences) versus log-odds. The *P* value in bold text is significant at $\alpha = 0.05$. Ordinary least-squared linear regression was used to determine the correlation between changes in record quality and observed geographic range selectivity. Raw data are available in SI Table 10.

*R^2 decreases to 0.12 if the end-Triassic and end-Cretaceous intervals are excluded and to 0.06 if the penultimate Cretaceous interval is also excluded. See text for discussion.

†Data from Peters and Foote (15); see *Data and Methods* for explanation of binning.

‡Data from the Exxon sea-level curve; see *Data and Methods* for explanation of binning.

To evaluate the impact of heterogeneous sampling on apparent geographic range selectivity, we compared observed odds ratios to changes in five metrics of record quality: (*i*) total number of occurrences in the PBDB; (*ii*) total number of tectonic plates in the PBDB; (*iii*) global sea level; (*iv*) number of named geological formations as a proxy for rock record completeness (15); and (*v*) the proportion of "range-through" genera, which are sampled before and after a given interval but not within it. Although changes in several of these metrics exhibit weak correlations with odds ratios, only the number of tectonic plates represented in the PBDB is both statistically significant at $\alpha = 0.05$ and explains >10% of the variance in log-odds (Table 1). The observed positive relationship largely reflects unusually intense sampling and/or data entry for mass extinction intervals, especially the latest Triassic and latest Cretaceous. Each of these intervals shows low selectivity and a substantial decrease in number of sampled plates going into the next time interval. Sampling of the latest Cretaceous is unusually complete in the PBDB, so the preceding interval also exhibits the largest increase in number of plates as well as substantial selectivity on geographic range. After excluding these three intervals, change in the number of plates explains only 6% of the variance in the log-odds, and the association is no longer statistically significant. Notably, the association between log-odds and change in the number of plates is positive, whereas we would generally expect an inverse relationship with selectivity, with narrowly distributed genera tending to exhibit last occurrences when sampling quality decreases into the subsequent interval. Decrease in the number of sampled plates in the subsequent interval would be expected to enhance the observed geographic range selectivity associated with these mass extinctions, but the end-Triassic and end-Cretaceous events exhibit the least geographic range selectivity in the entire data set. The number of named geological formations and the proportion of range-through genera exhibit marginally significant associations with selectivity, but neither explains >8% of the variance in log-odds.

In addition to differences in overall sampling intensity between time bins, there is very substantial regional variability in sampling intensity within each time bin. However, because extinction selectivity is evaluated independently in each time bin, these differences would only bias our results if widespread

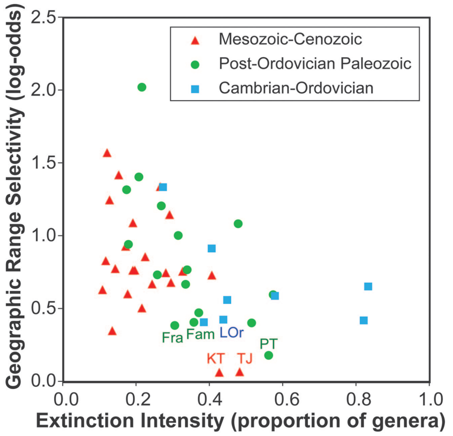

Fig. 2. Geographic range selectivity versus extinction intensity. Note that extinction intensity is generally high in the Cambrian–Ordovician and low in the Mesozoic and Cenozoic. Selectivity exhibits a weak inverse association with extinction intensity, which is discussed in the text. Log-odds are from the single regression of geographic range. Abbreviations are as in Fig. 1.

genera were either preferentially reported or underreported on each plate. In the absence of such an effect, there is no reason to believe *a priori* that geographic heterogeneity in sampling intensity within a time interval should bias observed extinction selectivity.

Range-through genera were not considered in the initial analysis because their geographic ranges are unknown. The most conservative approach is to assign each a range of a single plate on the assumption that they are not sampled because their ranges are narrow. Despite imposing a bias against finding selective survivorship of wide-ranging genera (because all range-through genera survive into the subsequent interval), this assumption does not substantially alter the observed geographic range selectivity (SI Table 6). Similarly, genera that occur in only one temporal bin (singletons) may bias the analysis in favor of finding an association between range and survivorship because many singletons may have existed for only a fraction of the interval and may be expected to exhibit particularly limited geographic ranges. Exclusion of singletons from the analysis does not substantially alter the magnitude or direction of geographic range selectivity (SI Table 7).

There is no unambiguous Phanerozoic-scale trend in the strength of association, but odds ratios estimating geographic range selectivity are lowest in association with three major mass extinction events, those at the Permian–Triassic (P–T), Triassic–Jurassic (T–J), and Cretaceous–Paleogene (K–T) boundaries (Fig. 1). There is a weak inverse correlation between extinction intensity and observed odds ratios (Fig. 2), although the P–T, T–J, and K–T events exhibit lower odds ratios than other intervals with similar extinction intensities. The Late Devonian exhibits similarly low geographic range selectivity in the multiple regression (Fig. 1*B*).

Discussion

The significant association between range and survivorship, even after controlling for species richness and occurrence frequency, confirms that geographic range has been an important determinant of extinction risk in the marine realm throughout Phanerozoic time. The significant range selectivity during background intervals observed in this study accords well with most previous studies of background extinction focused on selected higher taxa over shorter time scales (11), but there are possible exceptions (e.g., ref. 16).

The inverse correlation between geographic range selectivity and extinction intensity (Fig. 2) occurs because extinction risk is more sensitive to geographic range when per-plate extinction intensity is low. To understand this relationship, consider the situation in which per-plate extinction risk is equal to q for all plates. For a genus occupying n plates, the probability of global extinction (Q) is q^n, the probability of survival is $1 - q^n$, and the odds of survival are $(1 - q^n)/q^n$. The odds ratio when the number of geographic regions is increased from n to $n + 1$ is equal to

$$\mathrm{OR} = [(1 - q^{n+1})/q^{n+1}]/[(1 - q^n)/q^n]. \quad \textbf{[1]}$$

The odds ratio approaches $1/q$ asymptotically as n increases. Thus, as extinction rate (per plate) increases, differences in geographic range among genera have a smaller effect on relative extinction risk. When the average per-plate extinction rate is 50%, each additional plate occupied by a genus provides a substantial opportunity for survival, whereas if the per-plate extinction rate is 99%, each additional plate has little effect on the odds of survival.

The expected relationship between geographic range and survivorship can be derived, assuming that extinction risk on a given plate is equivalent for all genera occupying it. In this case, global extinction risk for a genus depends only on the number of plates it occupies and its likelihood of extinction on each of those plates. The probability of global extinction (Q) for a genus occupying n plates is

$$Q = q_1{*}q_2{*}\ldots{*}q_n, \quad \textbf{[2]}$$

where $q_1, q_2, \ldots q_n$ are the probabilities of local extinction on plates 1 through n. This model assumes that, although some plates may exhibit higher extinction rates than others, no genus is preferentially susceptible to local extinction on any given plate. Therefore, it is a null model in which ecological and physiological attributes are assumed to have no net effect on extinction risk; no genus is assumed to be more or less susceptible to extinction than any other, regardless of extinction-causing process. We calculated the expected odds ratios under the assumption of equal extinction risk among genera by using the extinction rates of endemic genera (genera occupying only a single plate) to estimate per-plate extinction rates for each plate during each 10 My interval (SI Table 8). We then assigned each genus a probability of global extinction based on the product of per-plate extinction rates on each plate that it occupied during the interval in question. By using the extinction rates of endemic genera to predict the expected extinction selectivity overall, we do not differentiate between true extinctions and apparent extinctions generated by variability of within-plate sampling through time. Thus, interval-to-interval variations in the sampling intensity of individual plates are implicitly accounted for in the calculation of expected odds ratios.

Extinction selectivity during many intervals is not demonstrably inconsistent with this null model; the 95% confidence intervals for observed geographic range odds ratios overlap the expected odds ratio in 20 of the 47 time intervals analyzed (Fig. 3). Thus, although the null model explains much of the observed pattern, it is clearly not a sufficient model of Phanerozoic geographic range selectivity. The majority of intervals exhibit odds ratios significantly lower than would be expected under the model of fully stochastic extinction and independence of extinction risk between plates. Among intervals that depart most from the null expectation are several of the major mass extinctions (Fig. 3) and a handful of other intervals of lesser extinction intensity but for which there is geological and paleontological evidence of widespread environmental perturbation.

Deviation from expectation under the null model of extinction risk suggests the existence of systematic differences in extinction

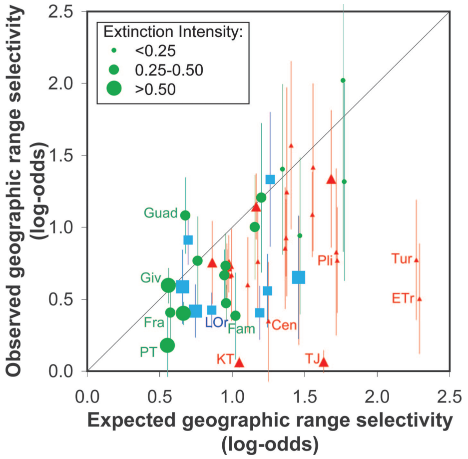

Fig. 3. Observed geographic range selectivity versus expected selectivity measured as log-odds if extinctions were entirely independent across plates. Intervals with less-than-expected geographic range selectivity are disproportionately intervals associated with geological evidence for widespread environmental disturbance. Geographic range selectivity values are from the univariate analysis. Abbreviations and symbols are as in Fig. 2. Cen, Cenomanian; Giv, Givetian; Guad, Guadalupian; Pli, Pliensbachian–Toarcian; Tur, Turonian–Santonian; ETr, Early Triassic.

risk among genera. This is not unreasonable; for most if not all extinction-causing processes, factors such as local abundance, body size, ecological guild, trophic level, motility, larval dispersal, and skeletal mineralogy are likely to influence extinction risk.

Over any 10-My interval, it is likely that multiple extinction-causing processes will operate on different plates and at different intensities. Thus, if p_{ij} is the probability that a genus on plate i survives disturbance j, the probability that the genus goes extinct during the interval (q_i) after m disturbances is

$$q_i = 1 - (p_{i1} * p_{i2} * p_{i3} \cdots * p_{im}), \qquad [3]$$

and q_i will be similar for all genera if no disturbance is strongly selective along alternative parameters or if multiple selective events produce a net extinction risk that is approximately equivalent across genera. When net extinction risk is not equivalent across all genera and particularly when net extinction risk differs systematically on many or all plates because of similar selectivity along ecological or physiological axes on each plate, differential extinction risk among genera will tend to reduce observed geographic range selectivity below the prediction of the null model.

The very weak geographic range selectivity associated with the P–T, T–J, and K–T mass extinctions (Figs. 1–3) suggests that per-plate extinction risk varied considerably among genera. Each of these events also is associated with geological and geochemical evidence for rapid, global environmental disruption coincident with geologically rapid extinction (17–27). Previous studies have identified ecological and physiological extinction selectivity patterns that may account for differences in per-plate extinction risk among genera during these intervals. End-Permian extinctions were selective on respiratory and skeletal physiology (28), end-Cretaceous extinctions were selective on feeding mode (10, 29), and end-Triassic extinctions were selective on local habitat preference (30). Although geographic range may have been an important control on extinction risk within ecologically or physiologically uniform sets of genera, systematic differences in extinction risk across the global fauna can explain the lower-than-expected range selectivity associated with these events.

The Late Ordovician and Late Devonian extinctions and several second-order events were more selective with respect to geographic range but still deviate significantly from expected selectivity. Geological evidence suggests that widespread environmental disturbances occurred at these times, although perhaps with less rapidity and intensity than during the K–T, T–J, and P–T events. These disturbances include glaciation during the Late Ordovician (31) and episodes of widespread anoxia in the Late Devonian (32–35), Pliensbachian–Toarcian, Cenomanian, and Turonian–Santonian (36). Although it is not a major mass extinction, persistent global-scale disturbance (37–39) also may explain low geographic range selectivity of Early Triassic extinctions (Fig. 3). At present, it is difficult to state what particular traits may be confounding geographic range selectivity in analyses of the global benthic fauna for these intervals, but geological evidence suggests that climatic and respiratory tolerances may provide useful insights. The Cambrian–Ordovician intervals of high extinction intensity are generally less selective than expected under the null model, possibly indicating a role for global-scale selective stresses. In particular, intense extinctions at the Early–Middle Cambrian and Cambrian–Ordovician boundaries exhibit below-expected selectivity, whereas the less intense extinction associated with the Middle–Late Cambrian boundary is consistent with a null model of stochastic extinction. Selectivity patterns suggest that, although diversity declines in the Late Devonian and across the Triassic–Jurassic boundary may reflect reduced origination rates as much as elevated extinction rates (1), the extinction components of these diversity declines may in fact reflect global-scale events.

The Guadalupian (Middle Permian) mass extinction exhibits pronounced selectivity on geographic range, suggesting that extinction-causing processes did not confound geographic range selectivity. Individual extinction-causing processes may have affected all genera equally, or the combined effects of many processes may have resulted in roughly equivalent per-plate extinction risk across all genera. The substantial selectivity of the Guadalupian and other intervals immediately preceding major mass extinctions also may reflect incomplete sampling of fossil occurrences. Of the genera that go extinct at any time, those with limited geographic ranges are more likely to be unsampled in their final interval of existence. Thus, among victims of the mass extinction, genera with limited range are more likely to appear to go extinct in an earlier bin than those with wide range. This artifactual increase in the proportion of narrowly distributed victims will increase the apparent geographic range selectivity of preextinction intervals and decrease the apparent range selectivity of mass extinctions. In the case of the Guadalupian, this effect may overprint the signature of a global extinction event (40). Although this effect can occur in any interval, it will be particularly pronounced when the subsequent interval contains a large number of extinctions.

The reduced geographic range selectivity associated with some mass extinctions and other intervals characterized by widespread environmental disturbance suggests that extinction during these intervals was dominated by one or a few processes that simultaneously imposed a similar set of selective stresses on many or all plates. Other intervals that exhibit greater geographic range selectivity are more likely to reflect the operation of many extinction-causing processes that, together, produce similar per-plate extinction risks for all genera. Although it is possible that these background processes also were rapid and global, this is not necessary: Background disturbances could operate at different times and places, each affecting only one or a few plates at a time. In the absence of geological evidence for widespread disturbances during background intervals, we hypothesize that most background extinctions primarily result from geographically limited processes.

Interestingly, intervals characterized by the least geographic range selectivity also are those that most significantly altered the ecological composition of marine communities (41–43). Because ecologically dominant taxa are commonly also widespread (44), extinctions characterized by pronounced geographic range selectivity are likely to result in the preferential survival of ecological incumbents. Therefore, most Phanerozoic intervals are likely characterized by the selective survival of ecologically dominant taxa. Ecologically severe mass extinctions may not selectively remove ecological incumbents, but they appear to be the only intervals when ecological incumbents are not disproportionately represented among survivors.

Conclusions

Geographic range appears to have been an important determinant of extinction risk throughout Phanerozoic time. Some variation in geographic range selectivity of genus extinctions can be accounted for strictly by variation in extinction intensity, and extinction patterns during many intervals are not demonstrably inconsistent with survivorship selectivity based on geographic range alone. Major mass extinctions and other intervals associated with geological and geochemical evidence of widespread disturbance are disproportionately represented among the intervals that deviate significantly from selectivity expected from range alone. We suggest that such deviation is most likely to arise from the application of similar ecological and/or physiological stresses simultaneously on most or all geographic regions, although it also may reflect factors such as differences in population sizes. This interpretation is supported by prior paleontological and geological studies indicating that mass extinctions linked to global-scale environmental disturbances exhibit strong ecological and/or physiological selectivity. Geographic range selectivity close to expectation during background intervals could reflect many regional or local-scale disturbances of varying selectivity or a single global-scale disturbance that increased per-plate extinction rates uniformly for all genera irrespective of ecology or physiology. Geological evidence suggests that most background extinctions reflect many disturbances but that few of these were of global extent. Therefore, we interpret our results as evidence that background and mass extinction differ in the geographic scale of primary extinction-causing processes. Although other factors clearly affect extinction risk during specific intervals, geographic range may be the most consistently significant predictor of extinction risk in the marine fossil record.

Data and Methods

Fossil Occurrences. Analyses are based on occurrence records of all Phanerozoic marine invertebrates downloaded from the PBDB (www.pbdb.org) on August 16, 2006. Occurrences not assignable to the standard 10-My bins in the PBDB were excluded from the analyses. We further confined the analyses to benthic taxa because pelagic/nektonic organisms often are subject to fundamentally different biogeographic and taphonomic regimes and therefore are inappropriate to analyze simultaneously with benthic taxa. The data set analyzed contains 227,229 occurrences of 12,300 benthic marine invertebrate genera from the Middle Cambrian through the Middle Miocene. We measured geographic range as the number of tectonic plates on which each genus occurred in each time bin. Tectonic plates were chosen because plate boundaries are likely to have been associated with biogeographic boundaries throughout the Phanerozoic and because estimates of paleolatitude and paleolongitude are more uncertain for older time intervals. Using a global equal-area grid as an alternative measure of geographic range returns a very similar selectivity trend (SI Table 9). To estimate species richness, we tabulated the number of named species for each genus in each time bin. Occurrences without a species name or designated as indeterminate species (e.g., sp. or spp.) were excluded from the calculation of species richness. However, genera not represented by any occurrences resolved to species level for a given time interval were assumed to be represented by one species. We also tabulated the number of occurrences in the database for each genus in each time interval. The earliest Cambrian interval was excluded from all analyses and figures because it contained too few genera and too few records to be suitable for statistical analysis. The most recent Cenozoic interval was excluded because it is impossible to evaluate survivorship without a subsequent interval. All other time intervals were included.

Selectivity. We evaluated selectivity of survivorship by using binary logistic regression (45). Relative risk estimated from logistic regression is expressed in the form of odds ratios, where an odds ratio of 1 [or log-odds of zero] indicates that the explanatory variable (e.g., geographic range) has no effect on extinction risk. An odds ratio of 2 indicates that each increase by one unit in the explanatory variable doubles the odds of genus survival [$p/(1-p)$, where p is the probability of survival]; an odds ratio of one-half indicates that each increase by one unit in the explanatory variable halves the odds of genus survival. The statistical significance of each analysis was determined by the degree to which the odds ratio differed from 1, because an odds ratio of 1 indicates no relationship between the response and explanatory variables. We used the odds ratio as our measure of selectivity. All figures plot the natural logarithm of the odds ratio so that effect strength is symmetrical whether the association is positive or inverse.

Logistic Regression. Logistic regression is a special case of a generalized linear model in which the link function is the logit: $\ln[p/(1-p)]$. It is applied in cases for which the response variable is binary (dichotomous) rather than continuous (45), such as extinction versus survival. The model is used to estimate the probability that a given observation will exhibit one outcome versus the other at a given value of the explanatory variable(s). The logistic function is widely used because of favorable mathematical properties and easily interpreted results (45). The approach assumes a monotonic relationship between p and the explanatory variable(s) and a linear relationship between the logit and the explanatory variable(s) (45). Estimation of model parameters does not follow the least-squares approach used in standard linear regression because variance does not remain constant for all levels of the explanatory variable(s). Instead, a maximum likelihood approach is used (45). We refer readers to Hosmer and Lemeshow (45) for a more detailed explanation of logistic regression and its applications.

Metrics of Record Quality. In addition to the three metrics of record quality based on the PBDB itself (number of occurrences, number of tectonic plates represented by at least one fossil occurrence, and percent range-through genera) we used data from Peters and Foote (46) and the Exxon sea-level curve [available at http://hydro.geosc.psu.edu/Sed_html/exxon.sea (accessed April 11, 2007)] to test for correlations between geographic range selectivity and changes in sedimentary rock volume and sea level. To compare these data directly to data in the PBDB, it is necessary to assign them to the same ≈10-My binning scheme. The North American named formations tallied by Peters and Foote (46) were binned primarily at the stage scale of resolution. We thus summed the number of formations in all stages that fall within each 10-My bin, using the cross-referencing of stages and 10-My bins in the PBDB as a guide. Because all but one of the bins used by Peters and Foote fall within the ranges of single 10-My bins, this is relatively straightforward. In a single case (the Eocene) a bin in Peters and Foote's data contains two PBDB 10-My bins. In this case, the total number of Eocene formations was used for both Cenozoic 2 and Cenozoic 3 based on the assumption that many formations span some or all of both intervals. Excluding the Eocene from the analysis has no significant effect on the observed correlation. The Exxon sea-level curve is resolved to intervals of 100,000 years, and, hence, sea level per 10-My bin was calculated by simply taking the average of all 100,000-yr intervals that fall within its boundaries.

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