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The Red Queen revisited: reevaluating the age selectivity of Phanerozoic marine genus extinctions

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Abstract.—Extinction risk is inversely related to genus age (time since first appearance) in most intervals of the Phanerozoic marine fossil record, in apparent contradiction to the macroevolutionary Red Queen's Hypothesis, which posits that extinction risk is independent of taxon age. Age-dependent increases in the mean species richness and geographic range of genera have been invoked to reconcile this genus-level observation with the presumed prevalence of Red Queen dynamics at the species level. Here we test these explanations with data from the Paleobiology Database. Multiple logistic regression demonstrates that the association of extinction risk with genus age is not adequately explained by species richness or geographic range: there is a residual association between age and extinction risk even when range and richness effects are accounted for. Throughout most of the Phanerozoic the age selectivity gradient is highest among the youngest age cohorts, whereas there is no association between age and extinction risk among older age cohorts. Some of the apparent age selectivity of extinction in the global fauna is attributable to differences in extinction rate among taxonomic groups, but extinction risk declines with genus age even within most taxonomic orders. Notable exceptions to this pattern include the Cambrian–Ordovician, latest Permian, Triassic, and Paleocene intervals. The association of age with extinction risk could reflect sampling heterogeneity or taxonomic practice more than biological reality, but at present it is difficult to evaluate or correct for such biases. Alternatively, the pattern may reflect consistent extinction selectivity on some as-yet unidentified covariate of genus age. Although this latter explanation is not compatible with a Red Queen model if most genus extinctions have resulted from biological interactions, it may be applicable if most genus extinctions have instead been caused by recurrent physical disturbances that repeatedly impose similar selective pressures.

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Introduction

Many factors have been suggested or shown to be associated with extinction risk in the fossil record (Raup 1992; McKinney 1997). Of these, perhaps the most controversial and least understood is taxon age. Following Simpson's (1944) observation that the mean age of living bivalve genera is greater than the mean duration of extinct bivalve genera, numerous workers have evaluated the relationship between taxon age and extinction risk in many groups and across widely varying time scales. In the most widely cited of these studies, Van Valen examined the age distributions of both living and extinct members of approximately 50 major clades, concluding that in nearly all cases extinction risk was independent of taxon age (Van Valen 1973). To explain this finding he proposed the Red Queen's Hypothesis: ''the effective environment of any homogenous group of organisms deteriorates at a stochastically constant rate'' and hence fitness at any given time—as measured by extinction risk—is independent of prior evolutionary success (Van Valen 1973).

Although the Red Queen's Hypothesis has been extremely influential, Van Valen's empirical determination that extinction risk is independent of taxon age has been challenged on methodological grounds (Foin et al. 1975; Raup 1975; Salthe 1975; Sepkoski 1975; Hallam 1976). Van Valen has responded to these criticisms (Van Valen 1976a, 1979), but subsequent analyses using different data sets and methodologies have usually found some association between taxon age (typically of families or genera, as in most of Van Valen's analyses) and extinction risk. This association is most commonly inverse—extinction risk declines as taxa age (Anstey 1978; Raup 1975, 1978a; Boyajian 1986, 1991; Jones and Nicol

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1986; Foote 1988, 2001a; Gilinsky 1988; Boyajian and Lutz 1992; Baumiller 1993) but some taxa, particularly planktonic groups, show an increase in extinction risk with taxon age (Hoffman and Kitchell 1984; Pearson 1992, 1995; Arnold et al. 1995; Doran et al. 2004, 2006). A minority of groups show no association between extinction risk and taxon age, most notably the Cenozoic mammals of North America (Foote and Miller 2007).

Taken at face value, these studies appear to contradict Van Valen's conclusion: extinction risk does tend to vary systematically with taxon age in most families and genera. However, the prevalence of age-dependent extinction dynamics among higher taxa does not necessarily imply that the same is true at the species level. Several factors have been suggested to reconcile these observations with the presumption of Red Queen (i.e., age-independent) extinction dynamics at the species level.

One such factor is geographic range. Genera tend to expand their geographic ranges through time (Willis 1922; Miller 1997), and widely distributed taxa are buffered against extinction (Jablonski 1986; Payne and Finnegan 2007; Wagner et al. 2007). Wide geographic range can be viewed as both a cause and a consequence of long duration: under a passive diffusion model of range expansion, genera that escape extinction will tend to widen their distribution through time, and this passive expansion will tend to reduce their risk of extinction in the future.

Species richness is, similarly, expected to be positively associated with genus age. All genera begin as single species and must maintain or increase species richness to avoid extinction. Hence, under a time-homogenous branching model of evolution, older genera will on average contain more species than younger genera (Raup et al. 1973), and will consequently be less susceptible to stochastic extinction even if extinction risk is independent of age at the species level (Raup 1978b; Flessa and Jablonski 1985; Boyajian 1991; Foote 2001a).

Finally, dynamic survivorship analyses based on the distributions of taxon durations suffer from a variety of statistical artifacts related to variation in extinction rates across time and among taxonomic groups (Van Valen 1973, 1976a,b, 1979; Raup and Sepkoski 1982; Van Valen and Boyajian 1987; Pearson 1992; Foote 2001a) (see Appendix for further discussion), and are further complicated by lack of knowledge regarding the ultimate durations of extant taxa (Van Valen 1979; Gilinsky 1988; Foote 2001a; Doran et al. 2004, 2006).

Various combinations of the above effects have been invoked to reconcile the age-dependent family and genus extinction patterns commonly observed in the fossil record with the age-independent species extinction regime posited by the Red Queen model, but there have been only limited efforts to evaluate their explanatory power. Consequently, more than three decades after the Red Queen's Hypothesis was initially proposed, it remains unclear whether Phanerozoic extinction patterns support an age-independent extinction model at the species level. There has been no attempt to explicitly examine the explanatory power of species richness and geographic range effects in accounting for the observed age selectivity of family and genus extinctions, largely owing to the absence of suitable data: studies subsequent to Van Valen's initial (1973) analysis have been based largely on Sepkoski's compendia (Sepkoski 1993, 2002) of biostratigraphic ranges for marine animal families and genera, which do not contain information on either geographic range or species richness.

The development of the geographically explicit, occurrence-based Paleobiology Database (PaleoDB) (Alroy et al. 2001) now permits direct evaluation of the influence of range and richness on genus extinction risk. Using data from the PaleoDB, we apply maximum-likelihood model selection to a series of nested logistic regression models to determine whether age-dependent increases in geographic range and species richness adequately account for the observed association between genus age and extinction risk, both in composite taxonomic samples and within individual orders. Our approach to the age selectivity question is different from that taken by preceding workers, in that the fundamental unit of our analysis is the extinction versus survival of genera across stratigraphic boundaries, rather than their ultimate durations. By evaluating extinction risk at each of 47 boundaries rather than drawing inferences from the cumulative distribution of genus durations, our analysis sidesteps many of the issues that have complicated previous survivorship analyses, particularly the confounding of age and time effects and censorship of the future durations of extant genera. In our analyses we address the following principal questions:

1. Does the inverse association between genus age and extinction risk simply reflect the positive associations between genus age and species richness and geographic range, or does it require additional explanation?
2. Is the association between genus age and extinction risk a simple monotonic function, or is the relationship more complex? Does it vary through time?
3. Is the association between genus age and extinction risk expressed within individual taxonomic orders as well as in the global composite fauna?

Data

Genera Included.—We evaluated the age dependence of genus extinction throughout the Phanerozoic by using the 280,048 occurrences of marine animal genera that were resolved within the 49 ~11-Myr bins in the PaleoDB as of 16 August 2006. Although they are of somewhat coarser resolution than stratigraphic stages, the PaleoDB time bins have the advantage that they are of approximately equal duration and thus reduce the potentially serious effects of uneven interval duration on survivorship analyses (Sepkoski 1975). We excluded genera that could not be assigned to a taxonomic order (often because they represent misspellings of valid genera), leaving 261,616 occurrences of 14,911 genera. Because we evaluated survivorship separately at each bin boundary, genera that occur in more than one bin are included in multiple analyses: in total there are 39,397 actual or potential boundary-crossing events (hereafter referred to as extinction/survival events) in the full data set, and the median number of genera evaluated at each bin boundary is 753.

Genus Age.—Following Foote (2001a), we measured genus age as the number of ~11-Myr bins from the first appearance of a genus (scored as 1) to the bin in which extinction selectivity is evaluated. Thus, for a given time bin B_t, the genera that first appear in that bin were assigned an age of 1, those that first appeared in the previous bin, B_{t-1}, and range into B_t were assigned age of 2, those that first appear in B_{t-2} and range into B_t were assigned an age of 3, etc.

Genera extant within a given time bin were scored as survivors if the genus was sampled in a subsequent time bin; otherwise they were scored as extinctions. The age-dependence of genus extinctions in the PaleoDB can be illustrated by compiling all extinction/survival events and comparing their relative proportions as a function of genus age (Fig. 1). Proportional extinction is highest among genera that first appear in a given interval and becomes successively lower for genera with longer prior stratigraphic ranges, showing little variation among genera older than ten time bins. Only 4% of all genera ever exceed this age, and many of these may be effectively ‘‘immortal’’ (Foote 2001b), representing either genuine lineages that are exceptionally extinction-resistant or the repeated convergent evolution of ecologically advantageous morphotypes (Plotnick and Wagner 2006; Wagner and Erwin 2006). Regardless of the reason for their persistence, these genera may exaggerate the apparent age selectivity of extinction by ensuring that extinction rates are always very low over a very large portion of the upper end of the potential age range. To reduce the influence of this long tail of old and highly extinction-resistant genera, we excluded all genera older than ten time bins when analyzing selectivity within each interval. Note that this is not equivalent to eliminating all genera with an ultimate *duration* greater than ten time bins: these genera were included in analyses for the first ten time bins of their range but were excluded from analyses in all subsequent intervals within their range. In addition, genera with a total duration of more than 25 bins were entirely removed from the data set, as many of these represent polyphyletic form genera (e.g., *Spirorbis*, *Lingula*). These culls leave 14,834 genera and 35,330 extinction/survival events.

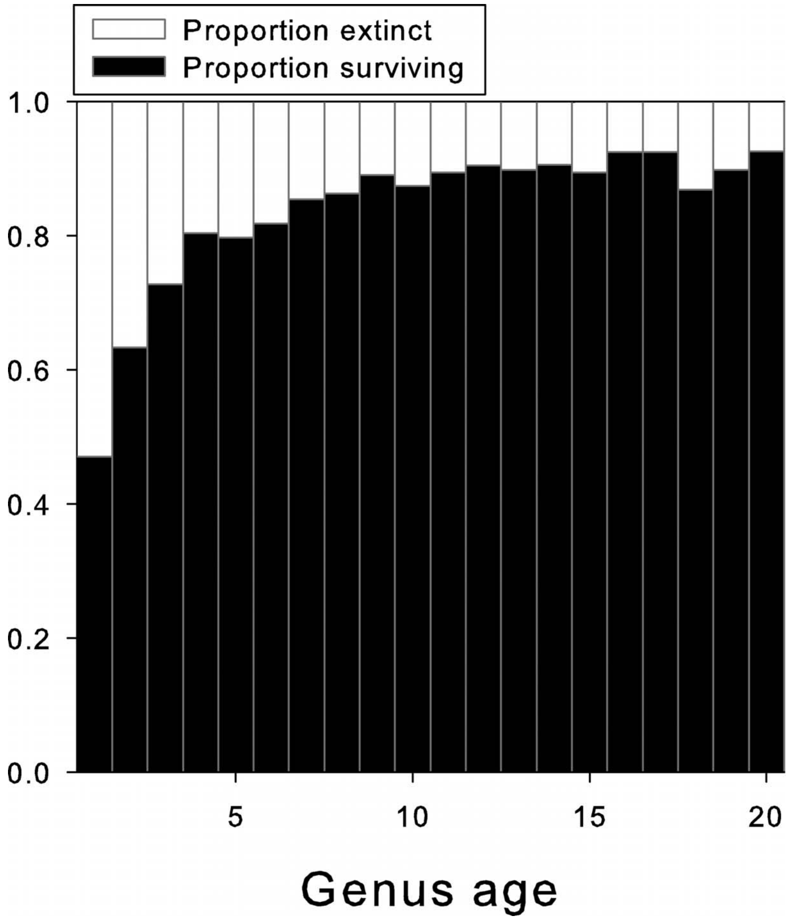

FIGURE 1. Selectivity of extinction with respect to genus age for all genera in the PaleoDB. Bars are scaled to the relative proportions of extinctions (white) versus survivals (black) for all extinction/survival events involving genera of the appropriate age. Because of the short duration of most genera, the relatively young age bins contain the great majority of extinction/survival events.

Species Richness and Geographic Range.—We tabulated species richness as the total number of named species recorded for each genus in each time bin; genera that had no species-level identifications within a given bin (i.e., genera in which species occurrences were only recorded as ''sp.,'' ''aff.,'' or ''cf.'') were assigned a minimal richness of one. Species reported as distinct but left in open nomenclature (e.g., *Zygospira* sp. A, *Zygospira* sp. B) were counted as separate species.

As a measure of geographic range, we counted the number of cells in a 10° by 10° paleolatitudinal-paleolongitudinal grid in which each genus occurs for each time bin. Although the precision of latitudinal and especially longitudinal paleocoordinates deteriorates with age, this measure of geographic range is strongly correlated with an alternative measure of geographic range that is independent of paleocoordinates, the number of tectonic plates occupied by each genus in each time bin ($R = 0.90$, $p < .001$).

Clearly, the absolute values of geographic range and species richness in any compilation of fossil occurrences will be highly sensitive to interval-to-interval variation in data coverage, with genera from well-sampled intervals tending to exhibit larger sampled geographic ranges and greater species richness than genera in poorly sampled intervals. However, it is important to emphasize the distinction between analyzing geographic range or species richness as absolute quantities and analyzing the strength of *association* between these variables and extinction risk. The goal of this study is not to estimate absolute changes in range or richness through time but, rather, to determine whether differences in these factors among genera *within a given time interval* adequately account for the association between extinction risk and genus age in that interval. Although it may be argued that sampling of richness and range degrade as a function of time before present, this bias, or any other time-dependent sampling bias, would affect the sampled range and richness of each genus similarly within any given time interval. To assess the relationship between range and/or richness and survivorship, it is only necessary to assume that differences in observed geographic range or species richness among genera within each time bin are proportional to the true differences in range and richness (see Appendix for additional discussion of the reliability of the data). Both species richness and geographic range were log transformed for all logistic regression analyses to reduce the influence of outliers, but using the untransformed linear variables has little effect on our results. For the sake of clarity, range and richness are presented as untransformed variables in the figures.

Range-Through Genera.—Genera that could be inferred via interpolation to have been extant in the time bin analyzed, but which were not sampled in that bin (''range-through'' genera) were assigned species richness and geographic range values drawn as paired values from the richness and range distributions of genera of the same age that belong to the same taxonomic order and, like the range-through genera, survive into the next time bin. This is conservative because it assumes that range-through genera, which by definition do not go extinct at the end of the interval, have the same geographic range and species richness distributions as the surviving genera that are actually sampled in a given time bin. In fact range-through genera are likely to have on average fewer species and more limited geographic distributions than sampled surviving genera; hence this assumption probably inflates the richness and range distributions of surviving genera and biases against finding any residual association between age and extinction risk (see Appendix for additional discussion of range-through genera).

Methods

We used binomial logistic regression (Hosmer and Lemeshow 2000) to evaluate multiple models of extinction selectivity across each of 47 boundaries in the time series of ~11-Myr bins (the first Cambrian time bin was excluded because of its very small sample size and the most recent time bin was excluded because it is impossible to evaluate extinction at the end of the time series). Most previous analyses of age selectivity have been based on the interpretation of survivorship curves for cohorts with a common time of origination (Raup 1978b; Jones and Nicol 1986; Foote 1988) or cumulative distributions of taxon durations (Van Valen 1973; Raup 1975). In addition to the well-known statistical artifacts associated with this approach (see Appendix for additional discussion), its major limitation is that it provides no statistical framework for examining the effects of confounding variables such as species richness or geographic range. Boyajian (1986, 1991) took an approach more comparable to ours in contrasting the age distributions of extinct and surviving families at several stage boundaries, but although he suggested that the age selectivity of family extinctions was attributable to species richness and geographic range effects, he did not test this hypothesis.

By evaluating extinction risk as a function of genus age separately at each bin boundary rather than inferring it from the distribution of ultimate genus durations, our approach avoids many of the pitfalls involved in interpreting cumulative survivorship curves. For example, it is not necessary to apply a correction factor to adjust for temporal variation in extinction rate (Holman 1983; Pearson 1992, 1995) if extinction patterns are considered separately for each time bin. Our approach is also unaffected by censoring of the future durations of living taxa (Gilinsky 1988; Foote 2001a) because it considers the *age* of a genus at the time of analysis, rather than its ultimate *duration*. Moreover, using the PaleoDB is advantageous because it reduces ''The Pull of the

Recent'' (Raup 1972): the PaleoDB contains records of fossil occurrences only, and hence it does not extend the biostratigraphic ranges of extant genera beyond their last fossil occurrences to the present day. Consequently, there is no systematic increase in the number of genera with interpolated biostratigraphic ranges as the Recent is approached.

Logistic regression is functionally analogous to ordinary linear regression, but it is designed for data in which the outcome is binary rather than continuous (Hosmer and Lemeshow 2000), such as extinction versus survival of a genus through a given interval. Logistic regression is used to model the probability, p, that a given observation will exhibit one outcome versus the other for a given value of the explanatory variable(s). The model assumes a monotonic relationship between p and the explanatory variable(s); more specifically, the logit $\ln[p/(1 - p)]$ and the explanatory variable(s) are assumed to have a linear relationship (Hosmer and Lemeshow 2000). Unlike ordinary linear regression, however, logistic regression does not assume homoscedasticity, nor does it assume normality of the residuals.

In logistic regression, the estimated association between a explanatory variable and the outcome is expressed in the form of an odds ratio. The odds ratio expresses the effect of an increase of one unit in the explanatory variable (in this case genus age, $\log_2$ geographic range, or $\log_2$ species richness) on the odds $[p/(1 - p)]$ of a successful outcome in the response variable, which is here measured as survival versus extinction of genera at each bin boundary. Odds ratios are analogous to slope coefficients in linear regression, and they can be expressed in comparable units by converting to a natural logarithm (log-odds), so that a value of zero indicates no association between the explanatory and response variables, whereas values above and below zero indicate positive and inverse associations, respectively.

As an example, consider two time bins, A and B, each of which has genera of two ages, 1 and 2. In time bin A the extinction rate is 30% for genera with an age of 1 and 20% for genera with an age of 2, whereas in time bin B the extinction rate is 30% for genera with an age of 1 and 40% for genera with an age of 2. In the first case the odds of survival for genera with an age of 1 are $0.70/0.30 = 2.33$ and the odds of survival for genera with an age of 2 are $0.80/0.20 = 4.00$, and therefore the odds ratio is $4.00/2.33 = 1.72$ and the log-odds is $\ln(1.72) = 0.54$. This positive log-odds value indicates that taxon age is positively associated with the probability of survival. In the second case the odds of survival for genera with an age of 2 are $0.60/0.40 = 1.50$, giving an odds ratio of $1.50/2.33 = 0.64$ and a log-odds of $\ln(0.64) = -0.44$. Here the negative log-odds value indicates that taxon age is inversely associated with the probability of survival. Thus, in all of our figures and tables log-odds greater than zero indicate disproportionate survival of older genera and extinction of younger genera and log-odds less than zero indicate disproportionate survival of younger genera and extinction of older genera.

Figure 2 illustrates the odds ratios and their relationship to survivorship patterns for three time bins, Devonian 3 (Eifelian–Givetian), Cretaceous 7 (Campanian), and Permian 4 (Wuchiapingian–Changhsingian). Note that the odds ratio is a measure of extinction selectivity, not overall extinction intensity. Although the overall extinction rate in Cretaceous 7 is less than half that of Devonian 3, Cretaceous 7 exhibits stronger selectivity in that a greater proportion of all extinctions occur among very young genera. Compared with both Devonian 3 and Cretaceous 7, Permian 4 exhibits only a very weak relationship between genus age and extinction risk.

In contrast to the least-squares approach used in ordinary linear regression, the logistic regression model is fit by using a maximum-likelihood estimation approach in which an iterative algorithm seeks to maximize the likelihood function (L). We used Akaike's modified information criterion ($\mathrm{AIC_c}$) to evaluate and compare goodness-of-fit for each of eight regression models accounting for all seven possible combinations of the three explanatory variables plus the possibility that there is no significant selectivity associated with any of the explanatory variables.

$\mathrm{AIC_c}$ values express goodness-of-fit while penalizing the addition of new parameters, which will always improve the fit of a multiple-regression model. Thus, the ''best'' model is the one that explains the most variation in the response variable with the fewest explanatory variables. AIC_c values were converted into Akaike weights (Burnham and Anderson 2002), which provide a proportional measure of the support for each model relative to all of the models considered—an Akaike weight of 0.75 indicates 75% confidence that a given model is the ''best'' model among all of the models considered. Akaike weights can be compared to determine the ratio of support (the evidence ratio) for one model or group of models versus another model or group of models. Akaike weights were summed for the four models that are consistent with an age-independent extinction regime (range, richness, range + richness, no selectivity) and for the four models that include an age term (age, age + richness, age + range, age + richness + range), and the cumulative weights were compared to measure the relative support for age-inclusive versus age-free models of extinction selectivity. Akaike weights were also used to produce a weighted average for the association between age and extinction risk from all four age-inclusive models.

Results

Association of Genus Age and Extinction Risk.- Extinction rates are significantly higher among young genera than among older genera extant in the same time bin for most Phanerozoic intervals. This age selectivity is expressed in Figure 3 as log-odds from a single logistic regression of extinction risk on genus age for each interval. Genus age is inversely associated with extinction risk (i.e., the log-

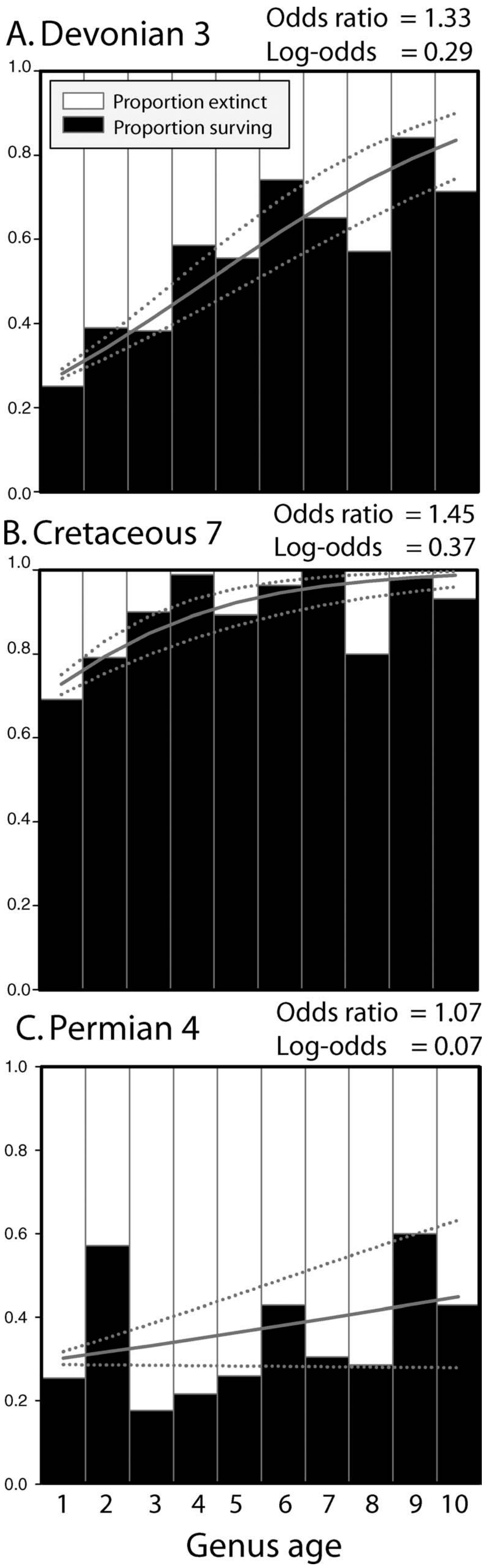

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Figure 2. Selectivity of extinction with respect to genus age for three time bins: Devonian 3 (A), Cretaceous 7 (B), and Permian 4 (C). As in Figure 1, bars are scaled to the relative proportions of extinctions (white) versus survivals (black) for all extinction/survival events involving genera of the appropriate age. Gray lines show the odds ratio estimate (solid line) and the upper and lower 95% confidence interval (dotted lines). Permian 4 exhibits the highest extinction intensity and the least selectivity with respect to genus age. Devonian 3 and Cretaceous 7 both exhibit relatively strong selectivity despite large differences in extinction intensity.

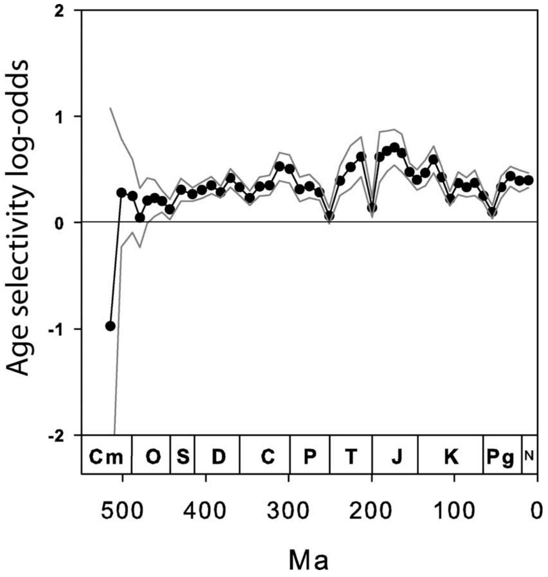

FIGURE 3. Age selectivity of extinction throughout the Phanerozoic. Log-odds estimates for the association between extinction risk and genus age (black dots) and 95% confidence intervals (gray lines) from logistic regression analyses of each ~11-Myr time bin in the Phanerozoic. Positive log-odds indicate that survival is highest among older genera, negative log-odds indicate survival is highest among younger genera, and log-odds near zero indicate no association between age and survival. Log-odds are significantly greater than zero in 41 out of 47 time bins, indicating that older genera are at lower risk of extinction. Cm = Cambrian, O = Ordovician, S = Silurian, D = Devonian, C = Carboniferous, P = Permian, T = Triassic, J = Jurassic, K = Cretaceous, Pg = Paleogene, N = Neogene.

odds is significantly above zero) in 87% of time bins, including every post-Ordovician time bin except for the terminal Permian (Table 1). The nonselective extinction model is rejected by an evidence ratio of at least 99:1 in all post-Ordovician time bins except for the terminal Permian, the terminal Triassic, and the Paleocene. The median log-odds for the association of genus age and extinction risk in all Phanerozoic time bins is 0.33 (odds ratio = 1.40), meaning that the odds of survival [$p/(1 - p)$] increase by 40% for each ~11 Myr of genus age. Note again that this does not imply that the *probability* of survival increases by 40%; rather, the *ratio* of surviving to extinct genera increases by 40% for each additional ~11 Myr of genus age.

Effects of Species Richness and Geographic Range on Age selectivity Estimates.—When all Phanerozoic genera are considered as a single sample, there is a tendency for mean species richness and mean geographic range to increase with genus age (Fig. 4A,B), as demonstrated in prior studies (Miller 1997). The association of genus age with species richness is similar to that of genus age with geographic range, reflecting the expected collinearity of geographic range and species richness under an allopatric speciation model (Mayr 1942).

Does the inverse association between genus age and extinction risk simply reflect the collinearity of age with geographic range and species richness? If so, after controlling for these variables there should be no residual association between age and extinction risk. However, this is not the case: extinction risk is highest for genera that are both young and narrowly distributed or species-poor, but there is a strong relationship between extinction risk and genus age across the entire spectrum of geographic range and species richness values (Fig. 5A,B). Extinction risk is also associated with geographic range and species richness among genera of all ages (Fig. 5A,B), as would be expected under most extinction models. Thus, at least in the composite sample of all extinction/survival events in the entire Phanerozoic, the association between extinction risk and genus age is not fully explained by geographic range or species richness. In contrast, the association of extinction risk with species richness does appear to reflect primarily the collinearity of richness and geographic range. There is relatively little residual association between species richness and extinction risk after controlling for geographic range (Fig. 5C), suggesting that species richness is the least significant of the three explanatory variables considered here.

That range and richness are insufficient to account for the association between age and extinction risk is illustrated by the multiple logistic regression models for each time bin: age-selectivity estimates when these variables are included (Fig. 6) are generally very similar to those given by the single-regression model based only on age (Fig. 3). When all possible combinations of range, richness, and age are considered, age-based models are still preferred by an evidence ratio greater than 99:1 in all post-Ordovician time bins except for the

TABLE 1. Akaike weights of logistic regression models for each time interval. The weight of the best model is in bold text.

		Akaike weight										
										Cumulative		Natural logarithm of evidence ratio
Interval	No. of genera	Age	Age + range	Age + richness	Age + range + richness	None	Range	Rich-ness	Range + richness	All age models	All age-free models	
Cenozoic 5	1264	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00	0.00	1.00E+00	1.55E−18	41.01
Cenozoic 4	1016	0.00	0.04	0.01	**0.95**	0.00	0.00	0.00	0.00	1.00E+00	2.42E−09	19.84
Cenozoic 3	1172	0.00	**0.73**	0.00	0.27	0.00	0.00	0.00	0.00	1.00E+00	6.22E−15	32.71
Cenozoic 2	1039	0.00	**0.70**	0.00	0.30	0.00	0.00	0.00	0.00	1.00E+00	3.72E−08	17.11
Cenozoic 1	952	0.00	**0.35**	0.00	0.29	0.00	0.20	0.00	0.16	6.42E−01	3.58E−01	0.58
Cretaceous 8	910	0.09	0.03	0.14	**0.74**	0.00	0.00	0.00	0.00	1.00E+00	9.23E−19	41.53
Cretaceous 7	746	0.00	**0.73**	0.00	0.27	0.00	0.00	0.00	0.00	1.00E+00	3.43E−10	21.79
Cretaceous 6	707	0.25	**0.43**	0.17	0.15	0.00	0.00	0.00	0.00	1.00E+00	2.57E−15	33.59
Cretaceous 5	656	**0.39**	0.15	0.32	0.14	0.00	0.00	0.00	0.00	1.00E+00	3.08E−15	33.41
Cretaceous 4	699	0.01	**0.47**	0.20	0.32	0.00	0.00	0.00	0.00	1.00E+00	4.68E−11	23.79
Cretaceous 3	610	0.22	0.16	**0.46**	0.17	0.00	0.00	0.00	0.00	1.00E+00	3.39E−21	47.13
Cretaceous 2	602	0.19	**0.49**	0.09	0.23	0.00	0.00	0.00	0.00	1.00E+00	4.49E−32	72.18
Cretaceous 1	596	**0.44**	0.26	0.20	0.10	0.00	0.00	0.00	0.00	1.00E+00	1.39E−20	45.72
Jurassic 6	670	0.01	**0.71**	0.02	0.26	0.00	0.00	0.00	0.00	1.00E+00	1.22E−19	43.55
Jurassic 5	1024	0.00	0.05	0.00	**0.95**	0.00	0.00	0.00	0.00	1.00E+00	5.64E−23	51.23
Jurassic 4	681	0.00	0.39	0.00	**0.61**	0.00	0.00	0.00	0.00	1.00E+00	9.81E−17	36.86
Jurassic 3	470	**0.42**	0.15	0.27	0.15	0.00	0.00	0.00	0.00	1.00E+00	4.10E−23	51.55
Jurassic 2	447	**0.44**	0.26	0.20	0.09	0.00	0.00	0.00	0.00	1.00E+00	3.81E−15	33.20
Jurassic 1	412	**0.40**	0.22	0.16	0.22	0.00	0.00	0.00	0.00	1.00E+00	2.19E−08	17.64
Triassic 4	595	0.02	0.07	**0.60**	0.22	0.00	0.01	0.06	0.02	9.08E−01	9.16E−02	2.29
Triassic 3	578	0.00	0.05	**0.51**	0.44	0.00	0.00	0.00	0.00	1.00E+00	3.47E−15	33.29
Triassic 2	491	**0.40**	0.27	0.14	0.19	0.00	0.00	0.00	0.00	1.00E+00	6.95E−10	21.09
Triassic 1	314	0.28	**0.32**	0.28	0.12	0.00	0.00	0.00	0.00	1.00E+00	1.48E−10	22.63
Permian 4	408	0.07	0.19	0.03	0.19	0.05	**0.23**	0.02	**0.23**	4.77E−01	5.23E−01	−0.09
Permian 3	662	0.00	**0.73**	0.00	0.27	0.00	0.00	0.00	0.00	1.00E+00	1.35E−08	18.12
Permian 2	570	0.00	0.11	0.00	**0.88**	0.00	0.00	0.00	0.00	1.00E+00	5.28E−08	16.76
Permian 1	440	0.00	0.13	0.22	**0.65**	0.00	0.00	0.00	0.00	1.00E+00	3.31E−06	12.62
Carbon. 5	440	0.00	0.34	0.00	**0.66**	0.00	0.00	0.00	0.00	1.00E+00	2.44E−14	31.34
Carbon. 4	458	0.00	0.29	0.14	**0.56**	0.00	0.00	0.00	0.00	1.00E+00	2.08E−19	43.02
Carbon. 3	486	0.00	0.29	0.14	**0.57**	0.00	0.00	0.00	0.00	1.00E+00	5.09E−14	30.61
Carbon. 2	546	0.00	**0.73**	0.00	0.27	0.00	0.00	0.00	0.00	1.00E+00	1.23E−13	29.73
Carbon. 1	626	0.00	0.48	0.00	**0.52**	0.00	0.00	0.00	0.00	1.00E+00	1.05E−09	20.67
Devonian 5	578	0.07	**0.62**	0.07	0.24	0.00	0.00	0.00	0.00	1.00E+00	7.62E−19	41.72
Devonian 4	628	0.03	0.06	**0.64**	0.27	0.00	0.00	0.00	0.00	1.00E+00	2.92E−26	58.80
Devonian 3	1135	0.00	0.03	0.00	**0.97**	0.00	0.00	0.00	0.00	1.00E+00	1.30E−14	31.97
Devonian 2	1063	0.00	**0.65**	0.00	0.35	0.00	0.00	0.00	0.00	1.00E+00	6.43E−13	28.07
Devonian 1	1137	0.00	**0.50**	0.00	0.50	0.00	0.00	0.00	0.00	1.00E+00	1.08E−09	20.65

TABLE 1. Continued.

Interval	No. of genera	Akaike weight								Cumulative		Natural logarithm of evidence ratio
		Age	Age + range	Age + richness	Age + range + richness	None	Range	Rich-ness	Range + richness	All age models	All age-free models	
Silurian 2	1500	0.00	**0.73**	0.00	0.27	0.00	0.00	0.00	0.00	1.00E+00	1.32E−08	18.14
Silurian 1	1021	0.00	0.14	0.00	**0.86**	0.00	0.00	0.00	0.00	1.00E+00	8.93E−06	11.63
Ordovician 5	1019	0.00	0.25	0.00	0.10	0.00	**0.46**	0.00	0.19	3.52E−01	6.48E−01	−0.61
Ordovician 4	1316	0.00	0.00	0.00	0.28	0.00	0.00	0.00	**0.72**	2.82E−01	7.18E−01	−0.93
Ordovician 3	803	0.00	0.02	0.00	0.25	0.00	0.06	0.00	**0.68**	2.67E−01	7.33E−01	−1.01
Ordovician 2	704	0.00	0.21	0.00	0.08	0.00	**0.50**	0.00	0.20	2.90E−01	7.10E−01	−0.90
Ordovician 1	451	0.00	0.07	0.00	0.19	0.00	0.20	0.00	**0.53**	2.68E−01	7.32E−01	−1.00
Cambrian 4	438	0.23	0.08	0.13	0.07	**0.24**	0.09	0.12	0.05	5.14E−01	4.86E−01	0.06
Cambrian 3	324	0.00	0.24	0.00	0.09	0.00	**0.49**	0.00	0.18	3.33E−01	6.67E−01	−0.69
Cambrian 2	451	0.00	0.00	0.00	**0.55**	0.00	0.00	0.00	0.44	5.55E−01	4.45E−01	0.22

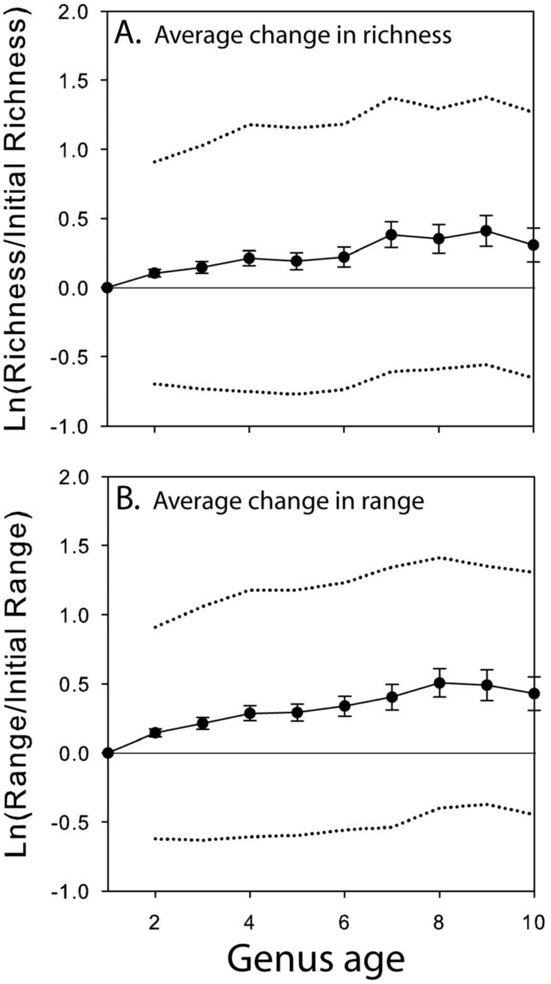

FIGURE 4. Dependence of species richness (A) and geographic range (B) on genus age, showing that genera tend to increase their richness and geographic range over time. The richness and range of each genus in each time bin was divided by the average richness and range for all genera in the time bin, to obtain measures of richness and range normalized to sampling intensity. Changes in range and richness throughout each genus's duration were quantified by dividing its normalized range and richness in each bin in which it occurs by its normalized range and richness in the bin in which it first appeared. A genus's geographic range and richness at a given age is thus expressed in multiples of its initial range and richness; this ratio is presented as a natural log to preserve the proportionality of positive and negative changes. Black dots are means with 95% confidence bars and dotted lines are 1 standard deviation on either side of the mean. Genus age is measured as number of ~11 Myr bins.

terminal Permian, the terminal Triassic, and the Paleocene (Table 1). Of the intervals in which an age-based model is not preferred, one of the models incorporating richness, range, or both is preferred over the nonselective (null) model by an evidence ratio >99:1 in most cases—the hypothesis of nonselective extinction can be rejected for all intervals except for the terminal Cambrian and the terminal Permian. In neither of these cases is there strong support for the nonselective model, which receives an Akaike weight of 0.24 for the terminal Cambrian and 0.05 for the terminal Permian.

The relative importance of each explanatory variable in controlling extinction risk can be evaluated for each time bin by comparing the Akaike weight of the complete model, including all explanatory variables, with the weight of a model lacking the variable of interest. For example, in Cenozoic 3 (Bartonian–Priabonian), the Akaike weight of the full model, age + range + richness, is 0.27, the weight of the age + range model is 0.73, the weight of the age + richness model is 4.3×10^{-8}, and the weight of the range + richness model is 1.8×10^{-15}. Hence the evidence ratio associated with adding age to the range + richness model is $0.27/1.8 \times 10^{-15} = 1.5 \times 10^{14}$, with adding range to the age + richness model is $0.27/4.3 \times 10^{-8} = 6.3 \times 10^{6}$, and with adding richness to the age + range model is $0.27/0.73 = 0.37$. In this case both range and age improve the model fit substantially, but species richness does not. Comparing such evidence ratios within all time bins gives an estimate of the overall explanatory power of each variable over the entire time series. By this criterion, species richness is the least important determinant of extinction risk: the evidence ratio associated with adding species richness ex-

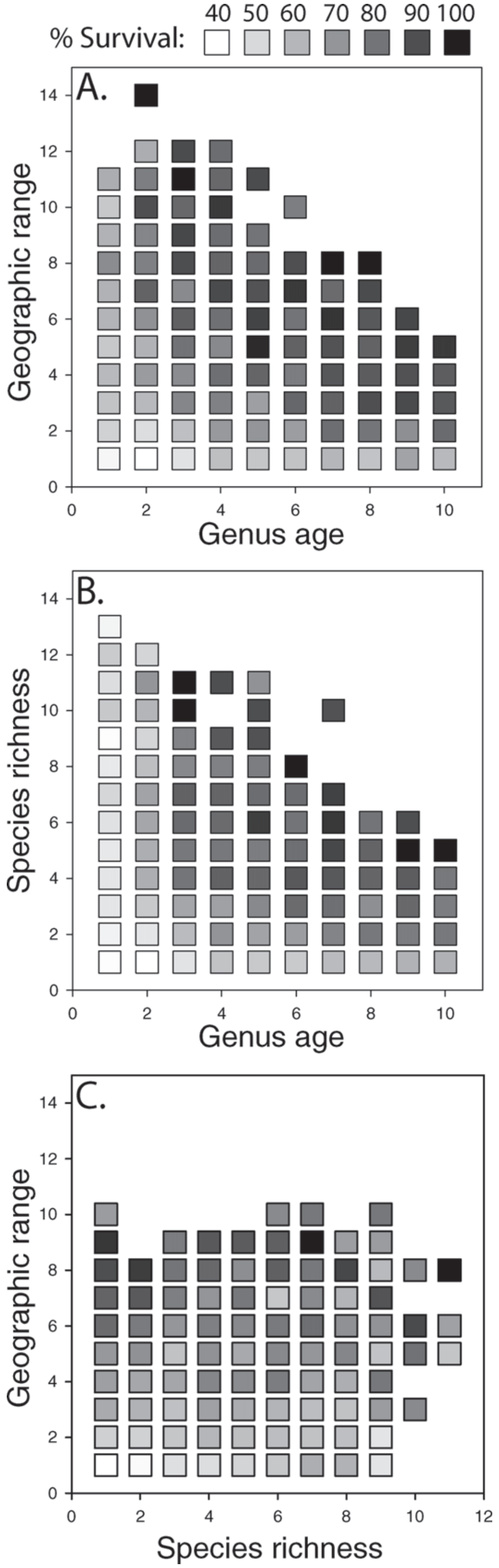

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FIGURE 5. Extinction risk as a function of age versus geographic range (A), age versus species richness (B), and geographic range versus species richness (C). Genus age is inversely associated with extinction risk, even after controlling for geographic range and species richness. All extinction/survival events were placed in bivariate bins (for example, all extinction/survival events involving genera with an age of 3 and a range of 4) and extinction risk was calculated as the proportion of extinctions among all extinction/survival events. Only bivariate bins that contained at least ten events were plotted. Darker shading signifies higher proportional survival, and lighter shading signifies higher proportional extinction (see key at top of figure).

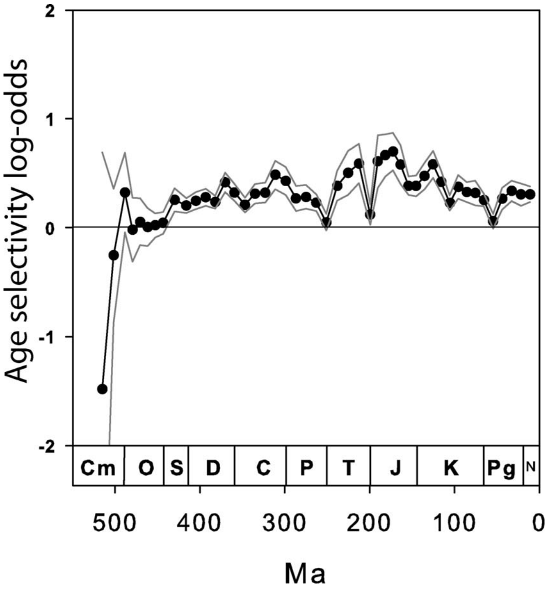

FIGURE 6. Age selectivity of extinction throughout the Phanerozoic after accounting for the effects of species richness and geographic range. Log-odds estimates for the association between extinction risk and genus age (black dots) and 95% confidence intervals (gray lines) from logistic regression analyses of each ~11-Myr time bin in the Phanerozoic. Log-odds and confidence intervals were averaged across all age-inclusive models according to their relative Akaike weights. Period abbreviations as in Figure 3. Note the similarity of this figure to Figure 1, indicating that little of the association between genus age and extinction risk is explained by geographic range or species richness.

ceeds 99:1 in only three time bins (6%), whereas comparable improvements in model fit are obtained by adding geographic range in 24 time bins (51%) and by adding genus age in 36 time bins (77%).

Consistency of Selectivity across Age Cohorts.— Logistic regression assumes that there is a linear relationship between the explanatory variables and the logit of the response variable, and hence attempts to describe the change in extinction risk with a single log-linear function. However, the association between genus age and extinction risk is not perfectly log-linear—rather, from the Silurian onward, extinction risk usually declines rapidly among the three youngest age cohorts and then levels off (Fig. 7). Hence, log-odds based on the simultaneous analysis of genera in all age cohorts are likely to imply a higher degree of selectivity among relatively old cohorts than is actually observed, especially given that regression slopes are weighted by the number of observations, most of which are in the youngest age cohorts.

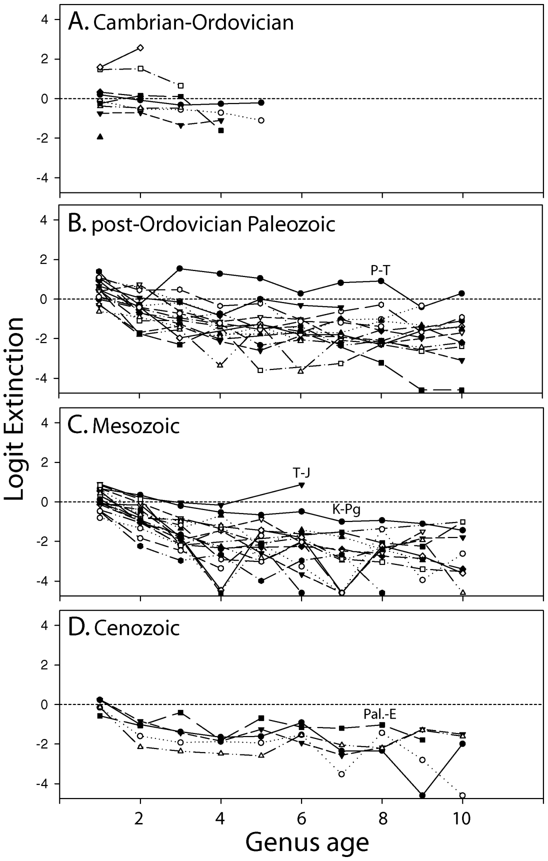

FIGURE 7. Decline in extinction risk as a function of genus age: the logit [$\ln(p/(1-p))$] of proportional extinction is plotted against genus age for each time bin in the Cambro-Ordovician (A), the post-Ordovician Paleozoic (B), the Mesozoic (C), and the Cenozoic (D). Dotted line represents 50% extinction. Initial indicate the stratigraphic boundaries presented by selected lines: P-T = Permian–Triassic, T-J = Triassic–Jurassic, K-Pg = Cretaceous–Paleogene, Pal.-E = Paleocene–Eocene. Each line connects logit(extinction) for each genus age cohort within a time interval. Logit(extinction) drops initially for younger genus age cohorts and then tends to level off as genus age increases.

To evaluate the consistency of selectivity across all age cohorts, we ran a series of multiple logistic regressions using the full model (age + richness + range) in which only adjacent age cohorts were compared (i.e., age 1 versus age 2, age 2 versus age 3, etc.) for all post-Ordovician time bins: if extinction risk changed as a linear function of genus age, we would expect the median log-odds to be com-

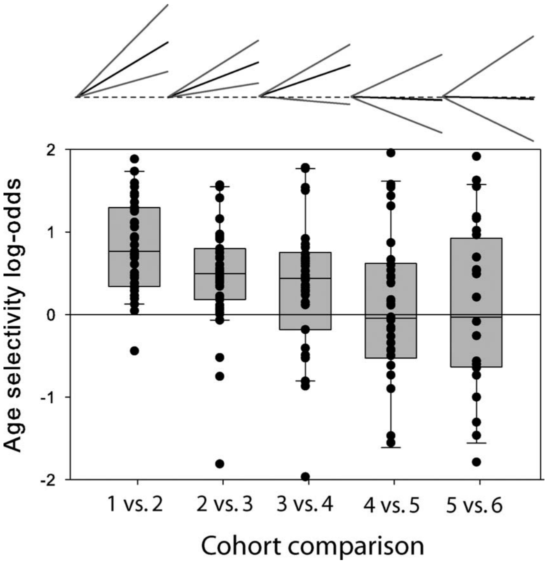

FIGURE 8. Selectivity of extinction between adjacent age cohorts. Log-odds are plotted for the association between age and extinction risk in comparisons of adjacent age cohorts (i.e., genera aged 2 versus genera aged 3) in each post-Ordovician time bin. The x-axis indicates which cohorts are included in each analysis, and black dots represent log-odds for the association of age and extinction risk between those cohorts, after accounting for range and richness effects, in each 11-Myr bin (for example, the difference in proportional extinction between genera with an age of 2 and genera with an age of 3 within the Devonian 3 time bin). Horizontal bars are medians, boxes enclose 25th and 75th percentiles, and whiskers are 5th and 95th percentiles. The median (black line) and 25th and 75th percentiles of the log-odds distribution (gray boxes) are also depicted as slopes across the top. The increasing variance of log-odds for older cohort comparisons reflects increasing uncertainty as sample sizes decrease. As suggested by Figure 7, age selectivity is greatest among in younger age cohorts and declines in older age cohorts.

parable for all such comparisons. Log-odds are generally high when age 1 and age 2 cohorts are compared (Fig. 8). Log-odds are lower but remain mostly positive when age 2 and age 3 cohorts are compared, and are lower still but dominantly positive for the age 3 to age 4 cohort comparison. Thereafter, however, there is no consistently identifiable association between age and extinction risk—the median log-odds is near zero for both the age 4 to age 5 and age 5 to age 6 comparison (relatively few time bins have sufficient numbers of older genera to make robust comparisons with genera aged 7 and older). Thus, the association between age and extinction risk is primarily limited to the youngest age cohorts, and is not consistently observed among genera with prior durations exceeding a few tens of millions of years.

This pattern is consistent with many dynamic survivorship analyses: taxa with relatively short durations are often overrepresented, but the frequency distributions of medium to long-ranging taxa are usually approximately log-linear (e.g., Anstey 1978; Baumiller 1993). We emphasize that these short-ranging taxa represent the majority of taxa at any given time—in the PaleoDB, only 20% of genera survive longer than three time bins. Hence, it may make sense to view the age-independence of extinction among older cohorts as the exception to the rule of age-selective extinction, rather than vice versa.

Selectivity among Taxonomic Orders.—Analyses of age selectivity and survivorship have often considered all marine invertebrates as a single composite sample, as we have thus far (Raup 1975, 1978b; Boyajian 1986, 1991), but Van Valen originally proposed that the Red Queen's Hypothesis applies only within ecologically homogeneous groups occupying the same adaptive zone (Van Valen 1973). In addition, it is possible to generate the appearance of age selectivity by mixing taxonomic groups with differing—but internally age-independent—extinction rates (see Appendix for additional discussion). Therefore, an analysis of the global fauna is not an adequate test of the Red Queen model.

Most of Van Valen's original examples of age-independent extinction rates concerned the age distributions of genera and families within classes and orders, which he considered to occupy similar adaptive zones in most cases. Hence, we analyzed the age selectivity of genus extinctions separately for each order within each time bin. We restricted the analysis to orders containing at least 30 genera for any given bin so that the ratio of observations to explanatory variables was at least 10:1, as has been recommended for logistic regression analyses (Peduzzi et al. 1996). This cull also reduces the influence of the imprecise selectivity estimates associated with very small sample sizes. Additional culling was necessary because in some cases all genera in the sample had identical values for one or more of the ex-

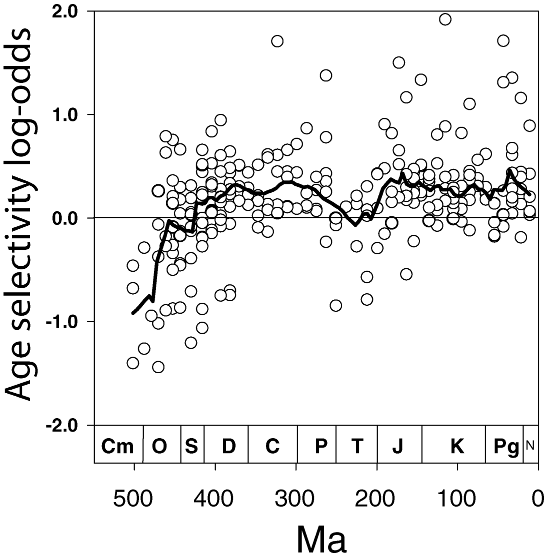

FIGURE 9. Age selectivity of extinction among taxonomic orders. Log-odds for the association between genus age and extinction risk are plotted for all orders having at least 30 genera and sufficient variation in age, range, and richness in each time bin. Log-odds determined by model averaging, as in Figure 5. Smoothing line is a loess regression (sampling proportion = 0.20). Period abbreviations as in Figure 3. Log-odds values are significantly greater than zero for most orders, suggesting that age selectivity is found even among genera inhabiting the same adaptive zone.

planatory variables or the response variable (e.g., all genera go extinct or all survive), making a maximum-likelihood estimate impossible (Albert and Anderson 1984). Of 1557 order–time bin combinations, 261 contained 30 or more genera and had sufficient variation in the explanatory variables to yield reliable likelihood estimates (see Supplementary Table 1 online at http://dx.doi.org/10.1666/07008.s1).

Most orders exhibit positive log-odds (i.e., an inverse association between genus age and extinction risk) even after accounting for the effects of range and richness (Fig. 9). The median weighted log-odds for the association between genus age and extinction risk among all orders and across all time bins is 0.21, somewhat lower than the median log-odds for composite samples. Although it is difficult to compare these numbers directly because of the much greater variation among orders, the predominance of positive log-odds at the ordinal level confirms that the age selectivity of extinction in the global composite fauna cannot be attributed primarily or simply to the effects of combining groups with different extinction rates (Appendix).

There are some important differences between the composite and the ordinal-level trends that are probably attributable to taxonomic mixing effects. In particular, whereas the Triassic, Jurassic, and Lower Cretaceous are characterized by relatively strong selectivity in the composite curve, the median age-selectivity log-odds of Jurassic and Lower Cretaceous orders are comparable to most other post-Ordovician intervals, and the log-odds associated with Triassic orders are notably low. The greater log-odds in the composite curve are likely related to the high diversity of cephalopods in the Mesozoic. Ammonoids in particular are characterized by very rapid evolutionary rates (Berg 1983), and hence when mixed with genera from slower-evolving groups will inflate the composite extinction rates of young age cohorts.

Because individual orders contain far fewer genera than the global composite sample, there is much greater uncertainty at this level and it is rarely possible to choose a single model or group of models with 99% confidence (Supplementary Table 1). We therefore relaxed the evidence ratio cutoff to 3:1, corresponding to a confidence level of 75% (i.e., there is a 75% or greater chance that the set of models including age predict extinction risk better than the set of models that exclude age). Nevertheless, it is difficult to select a model set in most cases: neither model set is preferred by an evidence ratio >3:1 in 186 out of 262 cases (71%). Among the order–time bin combinations for which one model set is preferred over the other by an evidence ratio of at least 3:1, the age-inclusive model set is preferred in five times as many cases (63) as the age-independent model (12). Moreover, this ratio increases sharply at higher evidence ratio cutoffs: if an evidence ratio cutoff of 4:1 is used the age-inclusive model set is preferred in 54 cases and the age-independent model set is never preferred. Thus, although the evidence is equivocal for many orders, when there is unequivocal evidence it nearly always favors models that include an age term.

Discussion

Suitability of Genera as Units of Analysis.—Although the Red Queen's hypothesis has primarily been applied to explain evolutionary patterns at the species level and below, only four of the compilations of taxon durations considered by Van Valen (1973) in formulating the law of constant extinctions were at the species level; the rest were at the genus and family levels. Genera are thus an appropriate unit of analysis for reconsidering this law. Raup (1975, 1978b) also considered genus-level survivorship data, and first pointed out the inverse relationship between lineage age and survivorship expected under a homogenous branching model of evolution and a stochastic extinction regime. Since Raup's work, this has been the prevailing explanation for the concavity of many survivorship curves. What has not been available up to this point are the species richness and geographic range data necessary to test the sufficiency of this model for multiple clades and time periods. Clearly, it would be in some ways preferable to examine the age selectivity of extinction in species directly, rather than the indirect approach taken here of examining genus extinction patterns and controlling for species richness and geographic range. However, there are major practical impediments to such analysis. Most species are short-ranging, so that even with fairly fine scale stratigraphic subdivisions the proportion of species that range through multiple stratigraphic intervals is usually quite small. Finer-scale subdivision can be achieved locally, but at this scale it is not always possible to differentiate between local extirpation and global extinction. New optimization-based biostratigraphic methods (Sadler 2004) hold great promise for ameliorating this limitation, but at present species-level survivorship analyses would be difficult and likely ambiguous for most invertebrate groups.

The most obvious exceptions to this limitation are planktonic microfossils, which are both widely distributed and represented by an exceptionally complete record. These provided the species-level data sets considered by Van Valen, and have subsequently been studied by several workers (Hoffman and Kitchell 1984; Pearson 1992, 1995; Arnold et al. 1995; Doran et al. 2004, 2006). Interestingly, several of these groups, most notably the Foraminifera, show a positive relationship between extinction risk and species age: extinction risk is lowest among the youngest species, especially (or only) following major extinction events (Pearson 1992, 1995; Doran et al. 2004, 2006). This is the opposite of the pattern commonly observed for invertebrate genera in this and other studies. Whether the difference is attributable to taxonomic level of analysis, to differences in taxonomic practice, or to ecological differences between planktonic microfauna and benthic macrofauna is an interesting area for further work.

Reliability of the Data.—Geographic range and species-richness data in the PaleoDB are coarsely resolved and incompletely sampled. Additionally, the stratigraphic ranges of genera in the PaleoDB often underrepresent their known ranges in the fossil record, and even their genuine first and last appearances in the fossil record may not represent true times of origination and extinction (Foote 2001b). These sampling biases can exert a strong effect on diversity analyses, and the ways in which they may also affect apparent selectivity patterns should be carefully considered.

There are significant uncertainties associated with all of the variables, but sampling of range and richness may be particularly problematic. It is possible, for example, that the uncertainty in range and richness estimates is greater than that in age estimates. In this case, the association of age with extinction risk could be spurious: age may appear to have an effect simply because the greater noise in range and richness degrades the correlation between these variables and extinction risk, leaving significant residual variation to be explained by age because it is independently correlated with these explanatory variables. We cannot rule this out, but we find it to be an unlikely explanation for the pattern. In simulations of this scenario (available upon request), the log-odds for the association between extinction risk and genus age are always substantially lower in the multiple-regression model than in the age-only model, and the confidence intervals wider. That is, although the noise in range and richness results in some of the true association between extinction risk and range/richness being spuriously partitioned onto age in the single-regression model, the strength of this association is always reduced when range and richness are also accounted for. However, accounting for range and richness actually has very little effect on age-selectivity log-odds estimates and their confidence intervals in most time bins (compare Figs. 3 and 6). Only in the Cambro-Ordovician are age-selectivity estimates substantially lower in the multiple-regression model than in the single-regression model. It thus seems improbable that the correlation between age and extinction risk is a spurious artifact of noise in range and richness.

In fact, the extinction selectivity associated with taxonomic age appears to be largely independent of the selectivity associated with range or richness (Fig. 5A,B). Extinction risk is significantly associated with both geographic range and species richness in most time bins when these variables are considered separately (Supplementary Fig. 1A,B, http://dx.doi.org/10.1666/07008.s2), and both remain significant predictors of extinction risk in many intervals even in the multiple-regression model including genus age (Supplementary Fig. 2A,B, http://dx.doi.org/10.1666/07008.s3), indicating that they are associated with extinction risk beyond their correlation with genus age.

It is also notable that the trend in age-selectivity log-odds is quite different from either range or richness selectivity trends (compare Supplementary Fig. 1A,B with Fig. 3). If genus age simply supplies a more precise estimate of range and/or richness, we should expect trends in age selectivity to parallel trends in range and richness selectivity, but this is not the case: the trend in extinction selectivity with respect to genus age is distinct from the selectivity trends associated with geographic range or species richness. Although range and richness selectivity trends are strongly correlated with one another ($R = 0.82$, $p < 0.001$), the age selectivity trend is not correlated with either range ($R = -0.02$, $p = 0.87$) or richness ($R = 0.06$, $p = 0.71$). Consequently, we suggest that observed extinction selectivity with respect to genus age in multiple-regression analyses is unlikely to reflect poor sampling of geographic range or species richness.

Other potential complications stem from uncertainty in the measurement of genus age and the timing of apparent versus actual extinctions. Some of the genera that first appear in any given time bin actually originated in prior bins, and some of the genera that last appear in that bin in fact persisted into subsequent time bins (Foote 2000). One way of evaluating our confidence that the first and last appearances of a genus in the PaleoDB reflect its actual origination and extinction is by measuring the completeness of its record within its known stratigraphic range (Foote 1997, 2001b; Foote and Raup 1996). Genera with a low probability of being sampled within their known stratigraphic range are also likely to have stratigraphic ranges substantially shorter than their true duration. If uncertainty about genus age and/or timing of extinction influences the association of genus age and extinction risk, then we expect there to be an association between the average sampling probability of genera within an order and the apparent age selectivity of extinction within that order.

To evaluate preservation probability, we calculated the proportion of all time bins within each genus's stratigraphic range for which the genus has at least one recorded occurrence in the PaleoDB. Because only internal occurrences can be meaningfully evaluated (FAD and LAD bins must be excluded) this limits the analysis to genera with durations of at least three bins. Each genus thus is scored from 1 to 0, with 1 signifying total completeness and 0 signifying total incompleteness. We averaged these scores for all genera in each order to produce an estimate of preservation probability at the ordinal level. We compared these estimates with the median log-odds for the association between genus age and extinction risk (controlling for range and richness) for all orders having at least 30 genera in at least one time bin (Supplementary Fig. 3; http://dx.doi.org/10.1666/07008.s4); there is no obvious correlation. As an additional test, we split genera in each time bin into two groups: those belonging to orders with above-average preservation probabilities and those belonging to orders with below-average preservation probabilities. There is no consistent difference in the log-odds for the association of genus age and extinction risk for these two groups (Supplementary Fig. 4; http://dx.doi.org/10.1666/07008.s5) again suggesting that apparent age selectivity is not strongly influenced by variation in the reliability of age estimates or by the backsmearing of last appearances.

Potential Effects of Taxonomic Artifacts.—Genus diversity data reflect a combination of biological, stratigraphic, and taxonomic signals, and hence taxonomic practice can potentially have a strong influence on survivorship. There are two primary type of taxonomic artifact to be concerned about.

It is likely that within any time slice, older genera contain a higher proportion of polyphyletic ''form'' genera, because the stratigraphic ranges of these genera may far exceed those of their constituent lineages. Such form genera are not necessarily biologically meaningless—in many cases they represent the iterative evolution of ecologically successful morphotypes (Plotnick and Wagner 2006; Wagner and Erwin 2006; Wagner et al. 2007)—but including them in survivorship analyses could create a spurious negative association between genus age and extinction risk. Wagner et al. (2007) determined that taxonomic standardization tended to increase extinction and origination rate estimates for Paleozoic gastropods (but affected only origination rate estimates for Jurassic bivalves and had little effect on origination or extinction rate estimates for Jurassic or Cenozoic bivalves). Although Wagner et al. did not examine stratigraphic ranges explicitly, the elevation of extinction and origination rates in the standardized Paleozoic gastropod data set implies a shortening of mean stratigraphic duration, likely due in part to the splitting of long-ranging polyphyletic genera. Their taxonomic standardizations also reduced the richnesses of the most speciose genera, many of which have quite long stratigraphic ranges. This implies that long-ranging polyphyletic genera also tend to be relatively speciose at any given time, and hence polyphyly alone may not account for the tendency of extinction risk to decline with age even among species-poor genera (Fig. 5B). Nevertheless, polyphyly cannot be ruled out as an explanation for the observed pattern without detailed taxonomic revision far beyond the scope of this study.

Although polyphyly is likely to extend stratigraphic ranges artificially, the durations of some lineages are prematurely truncated by paraphyly—the genus ceases to occur in younger strata not because of lineage extinction but rather because after some point in time the species in the lineage are sufficiently morphologically distinct from their ancestors that they are removed from it and assigned to a new genus (Simpson 1944; Van Valen 1973; Boucot 1978; Stanley 1979). It has been suggested that pseudo-extinction of paraphyletic taxa artificially inflates turnover rates (Smith and Patterson 1988; Forey 2004), but Uhen (1996) studied both simulations and empirical data on mammal families and found that paraphyletic taxa are actually often more extinction resistant than monophyletic taxa; other simulation (Robeck et al. 2000; Sepkoski and Kendrick 1993) and empirical studies (Wagner 1995) have found that paraphyletic taxa generally do not increase overall extinction probabilities.

The effect of pseudo-extinction on the association between taxonomic age and extinction risk depends not on its overall prevalence but on its frequency distribution with respect to age. Pseudo-extinction is often assumed to be more common in older genera, an assumption that would tend to create a positive association between age and extinction risk. Although this has been observed in some groups (Pearson 1992, 1995; Doran et al. 2004, 2006), it is the opposite of the pattern we observe for most groups in most time intervals. Pseudoextinction could only contribute to a *negative* association between extinction risk and genus age if it occurred more frequently in recently originated genera. Such an association could exist, if there is sufficient variation in rates of morphological evolution such that, within each cohort of originating genera, some subset of genera is likely to experience pseudoextinction before the other genera in its cohort. Under this scenario the proportion of each cohort composed of rapidly evolving lineages would decline as the cohort ages, and hence extinction risk would again appear to decrease with genus age at any given time.

A third possible source of bias is erroneous taxonomy. Smith and Jeffery (1998) found that taxonomic standardization of a database of Cretaceous–Paleogene echinoid occurrences resulted in a marked decrease in the apparent selectivity of extinction with respect to geographic range. They attributed this to a taxonomic misidentification bias that occurs when species that should properly be assigned to existing genera are instead assigned to newly erected genera. The resulting junior synonym is usually recognized only in a limited area, and will also be very likely to go ''extinct'' in the following time bin because surviving species will instead be properly assigned to the senior synonym.

Although Smith and Jeffery considered only geographic range selectivity, it is clear that such a bias would have a similar effect on species richness and genus age selectivity patterns. There is again no way to address this problem directly at the scale of this study. However, this bias would result primarily in an inflation of the proportion of singleton genera, and hence should have little effect on extinction rates in older age cohorts. The fact that extinction is age selective even when the youngest age cohort is excluded (Fig. 8) suggests that erroneous taxonomy is not a dominant component of the association between age and extinction risk.

Possible Evolutionary Explanations.—If the pattern does reflect, at least in part, a genuine positive association between genus age and average evolutionary fitness, there are two modes by which this could occur. There could in theory be a tendency for the average fitness of species themselves to increase throughout their duration, so that the relative fitness of the genus as a whole increases with time. Alternatively, and in our opinion more plausibly, the inverse association of extinction risk and genus age could reflect the accumulation of genera with extinction-resistant traits in older age cohorts, even if there is no tendency for the fitness of species *within* those genera to increase through time. This pattern would be expected if extinction were acting selectively on some as-yet-undetermined trait—such as environmental range or dietary flexibility—such that species with unfavorable trait states were culled by extinction early in the history of a given age cohort. This would be expressed most strongly at the genus level if the trait in question is highly conservative, so that species in the genus tend to give rise to new species with similar traits.

In both cases the mean fitness of the global fauna would tend to increase through time. Without detailed species-level phylogenetic information it is not possible to distinguish between the microevolutionary mode of fitness increase within species and the macroevolutionary mode of species (or genus) selection (sensu Stanley 1979). However, neither mode is consistent with the Red Queen's Hypothesis, because in both cases prior duration is an important determinant of extinction risk at any given time.

What then does the age selectivity of genus extinctions imply about extinction dynamics and the veracity of the Red Queen's Hypothesis? Despite its macroevolutionary origins, the Red Queen's hypothesis has had its greatest impact on microevolutionary and ecological theory (Dawkins and Krebs 1979; Stenseth and Maynard-Smith 1984; Dieckmann et al. 1995; Clay and Kover 1996; Marrow et al. 1996; Warwick and Clarke 1996), and it is therefore helpful to consider it as two related but distinct hypotheses (Lively 1996): a ''microevolutionary Red Queen'' concerned with the effect of biological competition on the production and maintenance of genetic variation (Lively 1996) and on community structure (Marrow et al. 1996), and a ''macroevolutionary Red Queen'' concerned with its effect on extinction risk.

Each hypothesis involves some metric of relative fitness, but measured in quite different ways. In the former case, fitness is measured directly as short-term reproductive success, whereas in the latter case fitness is inferred from taxonomic survivorship on geological time scales. Although taxonomic survivorship is contingent on reproductive success, it is difficult to scale short-term reproductive success to geological time scales because rare events have a disproportionate influence on geological and macroevolutionary processes (Gretener 1967; Raup 1991). Thus, even though there is abundant evidence that microevolutionary Red Queen dynamics are a pervasive feature of coevolutionary systems in nature (see references above, as well as numerous others) it is by no means clear that similar dynamics should be observed at the macroevolutionary scale.

To explain the disparity between microevolutionary process and macroevolutionary pattern, it may be helpful to consider the expected differences between biologically driven and physically driven extinctions. In their synthesis of the Red Queen's Hypothesis with island biogeographic theory (MacArthur and Wilson 1967) and species packing and limiting similarity theory (MacArthur and Levins 1964), Stenseth and Maynard Smith (1984) concluded that two end-member states are most likely to characterize the evolution of multispecies systems on geological time scales: a ''Red Queen'' state, dominated by biological interactions and exhibiting fairly constant rates of origination and extinction, or a so-called ''stationary'' state dominated by physical perturbations and exhibiting pulsed extinction and origination.

Organism-organism and organism-environment interactions differ critically in that only the former are symmetrical and escalatory. Red Queen dynamics are predicted to arise in biological systems because all components of the system are involved in a zero-sum competition for energy: a new adaptation that allows one species to increase its share of available energy decreases the amount of energy available to competitor species, which adapt in response. In such a system it is difficult for one species to maintain a consistent fitness advantage over evolutionary time scales. Hence, if biological interactions dominate long-term ecological dynamics and extinction ultimately results from failure to compete successfully (the Red Queen state), prior evolutionary success does not predict present extinction risk.

There is no comparable adaptive symmetry in the interactions between a species and its physical environment: the species evolves to adapt to its environment, but, with a few important exceptions, the environment itself does not change meaningfully in response. Thus, organism-environment interactions do not have the escalatory quality of organism–organism interactions. Whereas the adaptive symmetry of biological interactions means that ability to outrun a predator at present does not guarantee the ability to escape predators in the future, the traits that allow a species to survive a given physical perturbation once (for example, ability to survive low-oxygen conditions) will also help it to survive comparable perturbations in the future. Although the *magnitude* of such perturbations is of course highly variable, their magnitude does not escalate in response to the ability of species to survive them. Moreover, in contrast to the essentially infinite and ever-changing variety of potential biological threats, the potential physical threats faced by species (fluctuations in temperature, salinity, ocean pH, oxygen availability, habitat availability, nutrient availability) are comparatively limited. Over geological time scales, species are likely to face many of the same physical threats over and over again (Hallam and Wignall 1997; Stanley 1990).

Thus, if a large proportion of extinctions are due to geologically frequent physical perturbations that repeatedly impose similar environmental stresses (the stationary state), some degree of age selectivity is expected. Prior duration should be negatively associated with extinction risk because long-ranging species are more likely to have previously faced—and survived—a given disturbance, and are therefore more likely to posses whichever physiological or ecological traits enhance the likelihood of survival when a similar perturbation recurs. Van Valen in fact noted this in his discussion of perturbations: ''It is the organisms in the adaptive zone that can link the perturbations across time in that the effects of one perturbation may depend on the effects of those before it. Species easily removed by one kind of perturbation are not there if it comes again soon, and may accumulate if it does not come for a long time'' (Van Valen 1973, p. 18). To this we add only that a single perturbation will rarely remove *all* of the species that are ill-suited to the conditions that it imposes; rather, each time the perturbation recurs it will remove some fraction of the most susceptible species and some smaller fraction of the less susceptible species. Under this model, some degree of age selectivity seems unavoidable, as the composition of the biota at any time will always have been shaped by previous perturbations.

The effect of an iterative culling mechanism would be greatly enhanced if the trait(s) in question were conserved at the genus level, as is commonly the case for many physiological and ecological and possibly even some macroecological traits (Jablonski 1987). Progressive culling might also explain the lack of a consistent relationship between extinction risk and genus age when the youngest age cohorts are excluded. Once a given cohort has passed through the selective filter multiple times, most of the genera that lack whichever traits promote survival will have been eliminated and extinction risk among the remaining genera will no longer show a strong association with age. Exceptionally rare events (for example, large bolide impacts or severe ocean acidification) would be expected to exhibit much less age selectivity because very few genera will have previously encountered the conditions that these events impose. Age selectivity is in fact very low for some, though not all, of the major mass extinctions (the most notable exception being the terminal Cretaceous).

Recent analyses of marine extinction and origination patterns and their relationships to changes in sea level also suggest a primarily physical mechanism for most extinctions. The close correlation between metrics of sea level and continental flooding and extinction rate, and similarities in the age distributions of sedimentary basins and marine genera suggest a primary role for relative sea level in controlling global extinction rates at many times (Peters and Foote 2002; Peters 2005, 2006). Further, correcting for variations in sampling intensity indicates that Phanerozoic extinctions (and originations) have been even more pulsed and episodic in time than suggested by the raw data (Foote 2005, 2007). All of these observations are more easily reconciled with a primarily physically driven extinction model than with the biologically driven extinction regime posited by the Red Queen model.

Some paleoecological evidence also suggests a dominant role for physical factors in driving most extinctions. The basic ecological structure of marine communities has often remained markedly stable for long intervals, suggesting that the ecological environment experienced by species does not necessarily deteriorate steadily through time (Morris et al. 1995; Bambach 2002; Bambach et al. 2002; Bush and Bambach 2004a,b; Wagner et al. 2006), contrary to the Red Queen's Hypothesis. Furthermore, only events as severe as the era-bounding mass extinctions may be sufficient to disrupt the large-scale ecological structure of communities (Bambach et al. 2002; McGhee et al. 2004).

Aside from the terminal Permian and terminal Triassic, age selectivity is notably low during the Cambro-Ordovician, the Triassic (though this is manifest only within orders), and the Paleocene. This is somewhat surprising—given that these intervals have exceptionally high origination rates and that young genera usually exhibit the highest extinction rates, we would expect them to exhibit strong selectivity. We have no favored interpretation of this pattern, but it is notable and perhaps worthy of further attention that the advantages of incumbency appear to be reduced or absent during these intervals of elevated origination.

As initially pointed out by Boyajian (1986), the age selectivity of extinction, whatever its fundamental causes, is an important component of the Phanerozoic decline in extinction rates of marine genera (Raup and Sepkoski 1982). Because our analysis suggests that this selectivity is not explained by species richness or geographic range effects, it supports the hypothesis that the decline in extinction rates reflects, at least in part, an increase in mean fitness (where fitness is defined simply as extinction resistance at the species level). Here it is important, once again, to distinguish between fitness with respect to biological competition and fitness with respect to physical perturbations. Although biological competition has likely driven an increase in *absolute* fitness, such that the average Cambrian species would be ill equipped to compete with the average Neogene species (Vermeij 2004), the *relative* competitive fitness distribution has likely remained static, constrained by microevolutionary Red Queen dynamics. Rather, mean fitness may have increased because repeated physical perturbations have culled the taxa that are least equipped to survive the conditions they impose, leading to a progressive accumulation of extinction-resistant taxa and a consequent decline in extinction rates through the Phanerozoic.

Summary

Within nearly all Phanerozoic time intervals, there is a significant inverse association between genus age and extinction risk, in contradiction to a Red Queen macroevolutionary model. Surprisingly, very little of this age selectivity is accounted for by the fact that older genera tend to be more species rich and wider ranging within any given interval. Extinction risk does not decline as a simple function of genus age but rather drops off rapidly among the youngest age cohorts and thereafter shows little relationship to age. Some of the age selectivity in the global fauna can be explained by combining higher taxa with differing intrinsic extinction rates in a single analysis, but a statistically significant age-selective signal remains even within many taxonomic orders. This pattern may be influenced by taxonomic artifacts, but this possibility is difficult to evaluate. Alternatively, we suggest that the association reflects selective extinction acting on some other, as-yet unidentified covariate(s) of genus age, resulting in the progressive accumulation of extinction-resistant species and genera. Such a pattern is difficult to reconcile with a Red Queen model in which most extinctions result from escalatory biological competition, but it is consistent with geological evidence for recurrent physical perturbations, rather than biological interactions, as the major drivers of extinction through the Phanerozoic. Red Queen dynamics may dominate much of evolutionary time, but large, infrequent disturbances of the physical environment appear to play a disproportionate role in macroevolutionary dynamics.

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Appendix

Analytical Artifacts Related to Mixing of Taxa and Time Intervals

A potentially important statistical artifact arises when genera from many higher taxonomic groups are combined in a single statistical sample, which we will hereafter refer to as a composite sample (Van Valen 1973, 1976a,b, 1979; Raup and Sepkoski 1982; Van Valen and Boyajian 1987; Foote 2001a). Taxa with characteristically high extinction rates contain proportionately more young genera than taxa with lower extinction rates, just as the mean age of individuals is lower in countries with high mortality rates than it is in countries with low mortality. Consequently, the younger genera in a composite sample are drawn disproportionately from taxa with high extinction rates, and will therefore be at greater risk of extinction than older genera even if extinction is entirely independent of age *within* higher taxa. On a standard semilogarithmic survivorship plot of genus age versus time this is expressed as concavity in the survivorship curve, resulting from the averaging of multiple taxon-specific survivorship curves, each of which is log-linear but which are characterized by differing exponential decay rates (Van Valen 1979; Holman 1983; Foote 2001a). The distinction between apparent age selectivity in the composite sample and genuine age selectivity within higher taxa is an important one, because under the Red Queen model extinction is predicted to be independent of age only within ecologically homogenous groups—for practical purposes usually considered to be orders or classes (Van Valen 1973).

Cumulative (or dynamic) survivorship analyses, which combine genera from many different time intervals in a single statistical sample, can suffer from a similar analytical artifact, attributable in this case to variation in extinction rates through time rather than among higher taxa. Because overall extinction rates have fallen through the Phanerozoic, Paleozoic genera are generally shorter lived than Meso-Cenozoic genera. Hence, in the Phanerozoic cumulative sample young genera will appear to be at greater risk of extinction than old genera because young age classes contain disproportionate numbers of genera that originated in the Paleozoic, when genera of *all* ages appear to have experienced higher extinction risk than in the Meso-Cenozoic. Cumulative survivorship analyses thus confound the effects of age and time (Holman 1983; Pearson 1992, 1995; Doran et al. 2004, 2006) in the same way that composite samples confound the effects of age and phylogeny. Cumulative survivorship analyses are also complicated by temporal variation in the duration of sampling bins (Sepkoski 1975) and by ''censoring'' of the future durations of extant genera: because we have no knowledge of how long extant genera will ultimately persist, the durations of these genera cannot be directly compared with those of extinct genera (Van Valen 1979; Gilinsky 1988; Foote 2001a; Doran et al. 2004, 2006). Our approach, which considers individual extinction/survival events rather than ultimate durations, does not suffer from these complications.

Accounting for Range-Through Genera

When comparing the relative effects of genus age, geographic range, and species richness, genera that are unsampled in one or more time bin between their first and last appearances (hereafter referred to as ''range-through'' genera) pose a potential problem. Although their existence can be inferred by range interpolation, it is impossible to evaluate the species richness or geographic range of a genus for an interval in which it is unsampled. Range-through genera are a combination of genera that, though documented in the literature, have not yet been entered into the PaleoDB and ''Lazarus'' genera (Flessa and Jablonski 1983) that are actually missing from the fossil record. As such, their distribution is strongly affected by sampling. The proportion of range-through genera would be expected to increase toward the present in the PaleoDB if, like the Sepkoski database, it incorporated intensive sampling of the living fauna. Instead, the proportion of range-through occurrences peaks in the late Paleozoic and Mesozoic and declines in the Cenozoic, reflecting both variation in sampling intensity and the edge effects associated with truncation of the time series late in the Cenozoic.

It is not reasonable to exclude range-through genera, given that they account for as much as 42% of extant genera in some time intervals (the maximum proportion of range-through genera in any interval rises to 46% if genera older than ten time bins are included, because these genera are much less likely than younger genera to have been sampled in the prior interval). Furthermore, many range-through occurrences are likely attributable to low richness and/or narrow geographic range; ignoring them would bias the sample by preferentially excluding narrowly distributed and/or species-poor genera that nonetheless escape extinction, inflating apparent extinction rates in low richness and narrow range classes and thereby artificially exaggerating the influence of range and richness on extinction risk. In addition, because range-through genera have necessarily passed through at least one bin boundary prior to the bin in which they go unsampled, their average age is greater than that of other genera in the same bin, and hence ignoring them biases the age distribution of the sample.

To address this issue we generated two alternative sets of simulated geographic range and species-richness values for range-through occurrences, designed to represent end-members in the spectrum of reasonable values. In the first case, all range-through genera in all time bins were assigned minimal richness and range values of 1, under the assumption that they were disproportionately dominated by species-poor and narrowly distributed genera. In the second case, range-through genera in each time bin were assigned richness and range values drawn randomly (as paired values, so that the association between richness and range is preserved) from the richness and range distributions of genera that are sampled in that time bin, belong to the same order as the range-though genus (or class, if there were no genera of equivalent age in the order), are of the same age and, like the range-through genus, survive into the next bin.

The latter case is an unrealistically conservative model, because it assumes that there is no difference in species richness or geographic range between the genera that are actually sampled and those that are not. This is almost certainly not true. Although it is impossible to evaluate directly the species richness and geographic range of genera in the intervals from which they are missing, it is interesting to note that low species richness and geographic range in one interval appear to be important predictors of the likelihood that a given genus will not be sampled in the subsequent interval: in 37 out of 47 time bins that directly precede bins with range-through genera (the two most recent time bins are excluded because of edge effects), mean richness and range are higher for genera that are sampled in the subsequent time bin than for genera that range through the subsequent bin but are unsampled within it. The impact of range-through occurrences on observed age-selectivity trends turns out to be quite minor (median log-odds = 0.29 using minimum range and richness values, 0.26 using maximum range and richness values). Because these results differ only slightly, we use maximum values in all analyses.

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