Adjusting global extinction rates to account for taxonomic susceptibility

Steve C. Wang and Andrew M. Bush

Abstract.—Studies of extinction in the fossil record commonly involve comparisons of taxonomic extinction rates, often expressed as the percentage of taxa (e.g., families or genera) going extinct in a time interval. Such extinction rates may be influenced by factors that do not reflect the intrinsic severity of an extinction trigger. Two identical triggering events (e.g., bolide impacts, sea level changes, volcanic eruptions) could lead to different taxonomic extinction rates depending on factors specific to the time interval in which they occur, such as the susceptibility of the fauna or flora to extinction, the stability of food webs, the positions of the continents, and so on. Thus, it is possible for an extinction event with a higher taxonomic extinction rate to be caused by an intrinsically less severe trigger, compared to an event with a lower taxonomic extinction rate.

Here, we isolate the effects of taxonomic susceptibility on extinction rates. Specifically, we quantify the extent to which the taxonomic extinction rate in a substage is elevated or depressed by the vulnerability to extinction of classes extant in that substage. Using a logistic regression model, we estimate that the taxonomic susceptibility of marine fauna to extinction has generally declined through the Phanerozoic, and we adjust the observed extinction rate in each substage to estimate the intrinsic extinction severity more accurately. We find that mass extinctions do not generally occur during intervals of unusually high susceptibility, although susceptibility sometimes increases in post-extinction recovery intervals. Furthermore, the susceptibility of specific animal classes to extinction is generally similar in times of background and mass extinction, providing no evidence for differing regimes of extinction selectivity. Finally, we find an inverse correlation between extinction rate within substages and the evenness of diversity of major taxonomic groups, but further analyses indicate that low evenness itself does not cause high rates of extinction.

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Introduction

Measuring extinction intensity by the percentage of taxa that go extinct is like measuring the strength of an earthquake by the amount of damage inflicted, either in lives lost or property destroyed. In actuality, the damage caused by an earthquake reflects two factors: the strength of the earthquake itself and the susceptibility of the local population and infrastructure. The former (*intensity of cause*) can be measured on the familiar Richter scale, but the latter (*intensity of effect*) is affected by factors like population density and the resistance of buildings to damage. From the standpoint of an earthquake's effects on society, the amount of damage is the more important variable, but for understanding the causes of an earthquake, its physical intensity must be known as well. Likewise, the proportion and identity of taxa going extinct in a geologic time interval determine the consequences of an extinction event for the history of life, but these rates are a measure of the intensity of effect, which may not directly reflect the intensity of cause. Given the same environmental conditions or extinction trigger, two faunas may have different extinction rates, just as two locations may suffer different amounts of death and damage from an earthquake of the same intensity. Here, we attempt to infer the intensity of cause of extinctions in the marine fossil record, at least in a partial fashion. Specifically, we focus on the potential of faunas of different taxonomic composition to suffer different extinction rates given causal triggers of similar physical intensity. Our goal is to answer the following questions: (1) Does the relationship between the intensity of cause and effect change in important ways through the

Phanerozoic, or among mass extinctions, recoveries, and background intervals? (2) Are there other ways, at a very broad scale, in which the changing taxonomic composition of the marine fauna affected extinction rates?

Other paleontologists have also examined the relationship between extinction rates and the changing composition of the marine biota, ascribing the Phanerozoic decline in extinction rates to a shift in dominance from taxa with high rates to those with low rates (Stanley 1979, 2007; Sepkoski 1984, 1991; Van Valen 1985, 1987; Gilinsky 1994). Our goal is not to replicate these efforts, but rather to analytically remove the effects of changing taxonomic composition on observed extinction rates, allowing us to see how changes in composition might bias our views of the intrinsic intensity of extinction triggers. For example, were the effects of some mass extinctions mitigated by a particularly extinction-resistant fauna? Were the effects of other mass extinctions especially severe because they affected extinction-prone taxa? We also introduce a method for analytically estimating how much of the decline in extinction rates resulted from the changing taxonomic composition of the marine biosphere.

Simpson's Paradox: Do Smokers Live Longer?

Comparisons of taxonomic extinction rates (whether using percentage extinction or another metric) are the basis of many quantitative studies of mass extinction events (e.g., Raup and Sepkoski 1982, 1984; Benton 1995; Wang 2003; Bambach et al. 2004; MacLeod 2004; Rohde and Muller 2005; Bambach 2006). However, such comparisons of aggregate extinction rates can be misleading. It is possible for one event to have a higher extinction rate for each of several subgroups within the data set, yet for another event to have a higher extinction rate for the data set as a whole. This apparent contradiction can appear when subgroups with different extinction rates change in relative abundance through time—a statistical artifact known as Simpson's paradox (Simpson 1951).

Examples of Simpson's paradox appear in the statistical literature on a variety of sub-

jects, including gender bias in graduate admissions (Bickel et al. 1975), airline on-time rates (Barnett 1994), and racial bias in capital punishment (Gross and Mauro 1984). A classic example of Simpson's paradox occurred in a study on heart disease and a follow-up study conducted 20 years later (Appleton et al. 1996). The authors found, surprisingly, that women who smoked had a *lower* death rate after 20 years than women who had never smoked (24% mortality rate versus 31%, respectively). Because this finding contradicted a priori medical knowledge, the authors investigated further, dividing the women into subgroups according to age. A different picture then emerged: the smokers' death rate equaled or exceeded the non-smokers' death rate in every age subgroup, as would be expected. Why, then, when the subgroups were aggregated, did smoking appear to increase longevity?

This apparent paradox occurred because the smokers' age distribution differed from that of the non-smokers. The non-smokers included a higher percentage of older women (who grew up when smoking among women was less common), and older women have inherently higher death rates regardless of whether or not they smoke. The smokers, on the other hand, disproportionately included younger women. Once age differences in the two groups were taken into account, it became clear that smoking did indeed increase mortality.

This kind of pattern defines Simpson's paradox: trends in aggregated percentages disappear or even reverse themselves when one partitions the data into subgroups, such as age groups. In this example, discovering Simpson's paradox was not difficult: the aggregated data were clearly misleading, because we knew a priori that smoking is detrimental to one's health. We also knew that age is related to mortality rate, so it was natural to separate the data into subgroups by age.

In other cases, however, Simpson's paradox can be more insidious. We may have no a priori belief that an aggregated data set is yielding a misleading conclusion, so we may not suspect a need to partition the data into subgroups. Even if we have reason to subdi-

TABLE 1. Diversity of major molluscan classes in the Ordovician (Ashgillian) and end-Permian (Djhulfian) mass extinctions. Columns give the number of genera going extinct in the interval (Extinct), total diversity in the interval (Diversity), and extinction rate (Percent) for each extinction event. These data demonstrate Simpson's paradox: the Permian has a higher intrinsic severity, because the extinction rate for each class is higher in the Permian than in the Ordovician. However, when the classes are combined, the overall molluscan extinction rate is higher in the Ordovician. This misleading effect occurs because the Ordovician fauna has a large number of extinction-susceptible cephalopods, whereas the Permian fauna has a large number of extinction-resistant gastropods. Data are from Sepkoski's genus compendium (2002), as compiled by Bambach (1999) and Bambach et al. (2004); non-integer counts are due to fractional allocation of poorly-resolved genera.

	Ordovician			Permian		
	Extinct	Diversity	Percent	Extinct	Diversity	Percent
Cephalopoda	77.9	103.9	75	37.3	48.3	77
Bivalvia	48.1	80.1	60.0	48.3	80.3	60.1
Gastropoda	31.6	73.6	43	52.2	101.2	52
Mollusca	157.6	257.6	61	137.8	229.8	60

vide the data, there may no natural criterion by which to do so. In the smoking example, if Simpson's paradox had not been evident when we partitioned the data by age, perhaps it might have arisen had we partitioned the data by geographic region, race, or some other factor. Because we cannot possibly account for (or have data for) all possible partitioning factors, it may be all but impossible to detect Simpson's paradox in some cases.

Simpson's Paradox: Ordovician vs. Permian Molluscs

Simpson's paradox can also arise in paleontological examples, thereby making comparisons of aggregate percentages misleading. Here we show that Simpson's paradox arises when comparing extinction rates for molluscs during the Ordovician (Ashgillian) and end-Permian (Djulfian) mass extinctions. We consider only the three most diverse classes within Mollusca: Cephalopoda, Gastropoda, and Bivalvia. Other molluscan classes (e.g., Monoplacophora, Polyplacophora, Scaphopoda) have relatively low diversity during these stages; including them would not substantially alter our point, and we omit them for simplicity. To measure the taxonomic severity of each extinction event, we use per-genus proportional extinction rate: the number of genera having their last appearance in the stage divided by total diversity in the stage, a metric commonly used in the literature. The data are from Sepkoski's genus compendium (2002), as compiled by Bambach (1999) and Bambach et al. (2004).

Considering all three classes combined, 61% of genera went extinct in the Ordovician extinction, compared to 60% in the Permian extinction (Table 1). Thus, it seems that the earlier extinction had a more severe effect on molluscan diversity, if only by a small amount (whether or not this difference is statistically significant is not important here). However, when each class is examined separately, the opposite conclusion holds: the Permian extinction was in fact more severe for each individual class, much more so for gastropods.

Even though a higher percentage of molluscan genera go extinct in the Ordovician extinction (higher intensity of effect), it is misleading to infer that this extinction event was intrinsically more severe than the Permian extinction (intensity of cause). Instead, the Ordovician had a higher proportion of extinction-susceptible taxa (cephalopods, which have the highest extinction rate in both intervals). If we compare only aggregated extinction rates, however, this conclusion is obscured because of Simpson's paradox. To infer intensity of cause, it is therefore necessary to account for the effect of changing taxonomic susceptibility of the fauna in each interval. See Figure 1 for a graphical explanation of how Simpson's paradox arises in this example.

Goals and Methods

In general, extinction rates in an interval are affected both by the susceptibility of the taxa present and by factors intrinsic to that interval (e.g., bolide impact, anoxia, climate). To accurately infer intrinsic extinction severity, it is
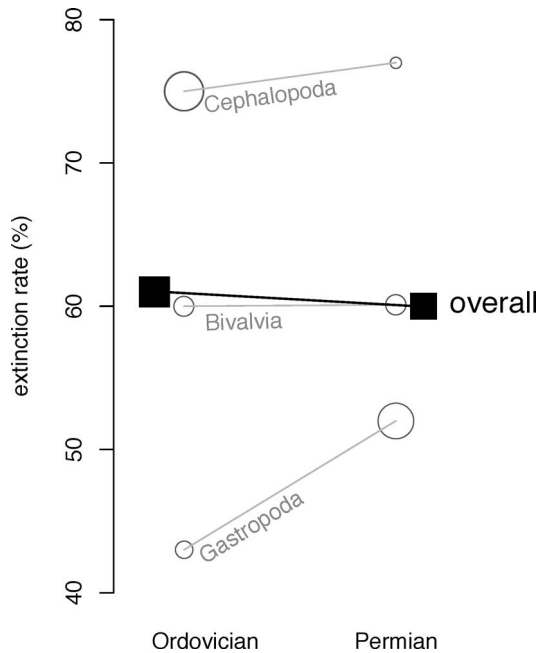
FIGURE 1. A visual representation of Simpson's paradox. For each class, the gray line indicates the genus-level extinction rates in the end-Ordovician (Ashgillian) and the end-Permian (Djhulfian) mass extinctions. The black line indicates the aggregated extinction rates in each mass extinction. Size of symbols indicates relative diversity (differences have been exaggerated for emphasis.) The end-Permian extinction was more severe for each of the three classes individually (upward-sloping gray lines). However, when the classes are aggregated, the end-Ordovician appears more severe overall (downward-sloping black line). This apparent paradox occurs because the aggregated Ordovician rate (black square at left) is pulled upward by the relatively high proportion of extinction-prone cephalopods (large circle at top left), compared to the relatively low proportion of extinction-resistant gastropods (small circle at bottom left). In contrast, the aggregated Permian rate (black square at right) is pulled downward by the relatively high proportion of gastropods (large circle at bottom right), compared to the relatively low proportion of cephalopods (small circle at top right).

important to account for taxonomic susceptibility, thereby reducing the possibility of equivocal or misleading findings due to Simpson's paradox. Our goal in this paper is to present a general framework for accounting for such effects at the class level and on a global scale over the Phanerozoic. On such a broad scale, Simpson's paradox in the strict sense described above is less likely to hold, given the large number of classes involved. However, it is nonetheless the case that the distribution of class susceptibilities can mitigate or exacer-

bate underlying extinction rates. To model such effects, we use an additive logistic regression model. In this model, the extinction rate of a given class in a given interval is modeled as a function of a class-specific susceptibility coefficient and an interval-specific severity coefficient. The interval-specific severity coefficients reflect the intrinsic extinction severity in each interval, after adjusting for the effects of taxonomic susceptibility. Our goal is analogous to that of demographers who calculate age-adjusted mortality rates for cities or other geographic areas: we adjust for differences in susceptibility of taxa in different time intervals in order to arrive at a susceptibility-adjusted extinction rate.

The Logistic Regression Model

A regression function is any function that models the relationship between the expected value (mean) of a response variable, Y, and one or more explanatory variables. A familiar example is linear regression, in which Y is quantitative. Logistic regression is analogous but used when Y is binary (dichotomous), taking on values that are typically labeled 0/1 or Success/Failure (Hosmer and Lemeshow 2000). In our case, Y represents whether a genus went extinct in a given interval, with $Y = 1$ indicating that the genus went extinct and $Y = 0$ indicating that it did not. For a 0/1 variable, the expected value is equal to the probability that $Y = 1$. This probability, which we denote by π_{it}, corresponds to the extinction rate of a genus in class i in substage t. To model π_{it} as a function of taxonomic susceptibility and substage-level effects, we use the following logistic regression model:

$$\pi_{it} = 1/\{1 + \exp[-(\beta + \kappa_i + \tau_t)]\}. \quad (1)$$

The left-hand side of this equation denotes the probability that a genus in class i goes extinct in substage t. The right-hand side is the logistic function applied to the sum $\beta + \kappa_i + \tau_t$, where the coefficient β represents the baseline extinction level for a genus in an average class in an average substage; κ_i represents the average extinction susceptibility of class i (that is, the propensity of a genus in class i to go extinct in an average Phanerozoic substage); and τ_t represents the extinction severity of

substage t (that is, the propensity of a genus in an average class to go extinct in substage t). (A helpful mnemonic is β = **B**aseline, κ = **C**lass, τ = **T**ime.) Applying the logistic function constrains the estimated values for π_{it} to lie between 0 and 1, as must be the case for probabilities. (We have chosen to scale the κ and τ coefficients so that zero represents an average class or substage. The coefficients may be scaled in other equivalent ways, but this choice is most intuitively interpretable.)

With some algebra, model (1) is equivalent to the following:

$$\log[\pi_{ij}/(1 - \pi_{ij})] = \beta + \kappa_i + \tau_{t.} \qquad (2)$$

The left-hand side of this equation represents the logarithm of the *odds* of extinction (i.e., the probability of extinction divided by the probability of survival) for a genus in class i in substage t. The log odds, also known as the *logit* of π_{it}, rescales the probability π_{it} over the entire real line. A probability greater than 0.5 corresponds to a positive logit value; a probability of 0.5 corresponds to a logit of zero; and a probability less than 0.5 corresponds to a negative logit.

This model assumes that intrinsic severity of each substage is the same for each class in that substage, and that the class and substage effects are additive, with no interactions between the two. These assumptions are obviously a simplification; below we investigate how well the model agrees with observed data.

In summary, the logistic regression model allows us to partition observed extinction levels for each genus in each interval into a component associated with the susceptibility of the class to which the genus belongs (κ_i) and a component associated with the intrinsic severity of that substage (τ_t). Using such a model, we avoid being misled by Simpson's paradox in inferring the intrinsic severity of extinctions in Phanerozoic substages. Instead, we are able to examine extinction severity through time in a way that is independent of changes in taxonomic composition. Similarly, we are able to estimate the extinction susceptibility of each class independently of the intervals in which they were extant.

As an example of how logistic regression

TABLE 2. Estimated β, κ, and τ coefficients from the logistic regression model given by equation (1), applied to the mollusc data in Table 1. These values were estimated by maximum likelihood using an iterative least-squares algorithm; calculations were carried out in R (R Development Core Team 2007). A, Extinction intensity for each substage, given both on a logit scale (τ_t) and on a probability scale (π_t). For instance, a genus in an average molluscan class has a 0.60 probability of going extinct in the Ordovician extinction and a 0.64 probability of going extinct in the Permian extinction. The logistic regression model controls for differences in the taxonomic susceptibility of fauna extant in an interval, thereby avoiding misleading conclusions due to Simpson's paradox (cf. Table 1). B, Extinction susceptibility for each class, given both on a logit scale (κ_i) and on a probability scale (π_i). For instance, a bivalve genus has a 0.60 probability of going extinct in an average substage (where "average" refers to the average of the Ordovician and Permian extinctions). Note that coefficients are normalized to sum to 0 on a logit scale.

A. Results by substage

	Ordovician	Permian
Coefficient τ_t	−0.088	0.088
Probability π_t	0.60	0.64

B. Results by class

	Bivalvia	Cephalopoda	Gastropoda
Coefficient κ_i	−0.086	0.673	−0.587
Probability π_i	0.60	0.76	0.48

partitions class and substage effects, we apply this technique to the mollusc data set in Table 1. The values of the β, κ, and τ coefficients do not have closed-form solutions, but they can be estimated by maximum likelihood using an iterative least-squares algorithm. For all analyses we used the software R (R Development Core Team 2007) for Mac OS X. Table 2 gives the estimated coefficients for each class and each substage. The estimated value of the baseline β equals 0.497.

These coefficients (τ_t and κ_i) are on the logit scale rather than the more intuitive probability scale. To convert these coefficients to probabilities (π), we use equation (1). For instance, the intrinsic extinction severity of the end-Permian, adjusted for taxonomic susceptibility, is calculated by substituting β = 0.497, κ = 0 (representing an average molluscan class), and τ = 0.088 into equation (1). Thus, a genus in an average molluscan class (that is, one having average extinction susceptibility) would be expected to have a $1/\{1 + \exp[-(0.497 + 0 + 0.088)]\}$ = 0.64 probability of extinction in

the end-Permian extinction. The other probabilities in the table are calculated similarly.

Molluscs had a higher aggregate extinction rate in the Ordovician extinction compared to the Permian extinction (Table 1). Once we adjust for taxonomic susceptibility, however, we see that the Permian extinction had a greater intensity of cause: the adjusted extinction rate was $\tau = 0.64$, compared to $\tau = 0.60$ for the Ordovician extinction, so a genus in an average molluscan class would be more likely to perish in the Permian extinction (Table 2). In the raw aggregated data (Table 1, Fig. 1), the true severity of the Permian is masked by the relatively lower taxonomic susceptibility of fauna extant in that interval—in particular by the relatively higher number of extinction-resistant gastropod genera and the lower number of extinction-prone cephalopod genera.

Table 2 also gives estimates for the κ_i coefficients on the logit scale and their corresponding probabilities. These values represent the extinction susceptibility of each class, with $\kappa = 0$ representing an average molluscan class. As expected, cephalopods have high susceptibility and gastropods have low susceptibility. Note that these probabilities do not necessarily equal the raw extinction rates for each class, as the latter may be skewed by the unequal distribution of the class in different extinction events. For instance, a class that reached its peak of diversity in the Late Permian may have a higher raw extinction rate than a class that peaked in the Ordovician, even if both classes have the same inherent extinction susceptibility. If a class is disproportionately represented in substages with high turnover, its observed extinction rate will overstate its true extinction susceptibility.

One might ask how logistic regression is able to separate the effect of each class from the effect of each substage. For example, if trilobites have an elevated extinction rate in the Ashgillian, is this a property of trilobites or a property of the Ashgillian? If each class were extant in only one substage, then separating the class effect and the substage effect would indeed be impossible. However, because there are multiple classes in each substage, and multiple substages for each class, there is sufficient information to distinguish class and substage effects. For example, we can examine Ashgillian extinction rates in other classes besides trilobites to see if they are elevated as well; if so, we are likely seeing a property of the Ashgillian rather than of any particular class. Similarly, we can examine trilobite extinction rates in other substages, particularly substages in which extinction rates are not generally elevated. If trilobite extinction rates in such substages are similarly high, then we are likely seeing a property of trilobites rather than of any particular substage.

In summary, the logistic regression model is able to distinguish taxon-level effects from interval-level effects. We are thus able to estimate extinction rates for each substage adjusted for taxonomic susceptibility, and to estimate extinction rates for genera in each class adjusted for relative diversity changes over time. We now apply these methods to global data over the entire Phanerozoic.

Data

We fit the logistic regression model given by equation (1) to genus-level data from 107 stages and substages (properly ages and subages, but henceforth referred to as substages as per common usage) from the Sepkoski compendium (Sepkoski 2002), as compiled by Bambach (1999) and Bambach et al. (2004). Many new diversity analyses currently use the Paleobiology Database (PBDB; http://paleodb. org) because it contains geographically explicit data that can be subsampled (e.g., Alroy et al. 2001; Krug and Patzkowsky 2007). We have chosen to use the older data of Sepkoski for several reasons. First, we wanted a large number of time intervals for our logistic regression, and in order to increase the amount of data within time bins, analyses of the PBDB are typically conducted at coarser temporal resolution than analyses of Sepkoski's data. Second, we wanted good coverage of rare and poorly preserved taxa, as well as common and robust taxa, and felt that this was better achieved with Sepkoski's data. To take advantage of subsampling, one must reduce sampling intensity in all time intervals to the level of the most poorly sampled time interval, and this would eliminate much information on some taxa. It could also increase the effects of
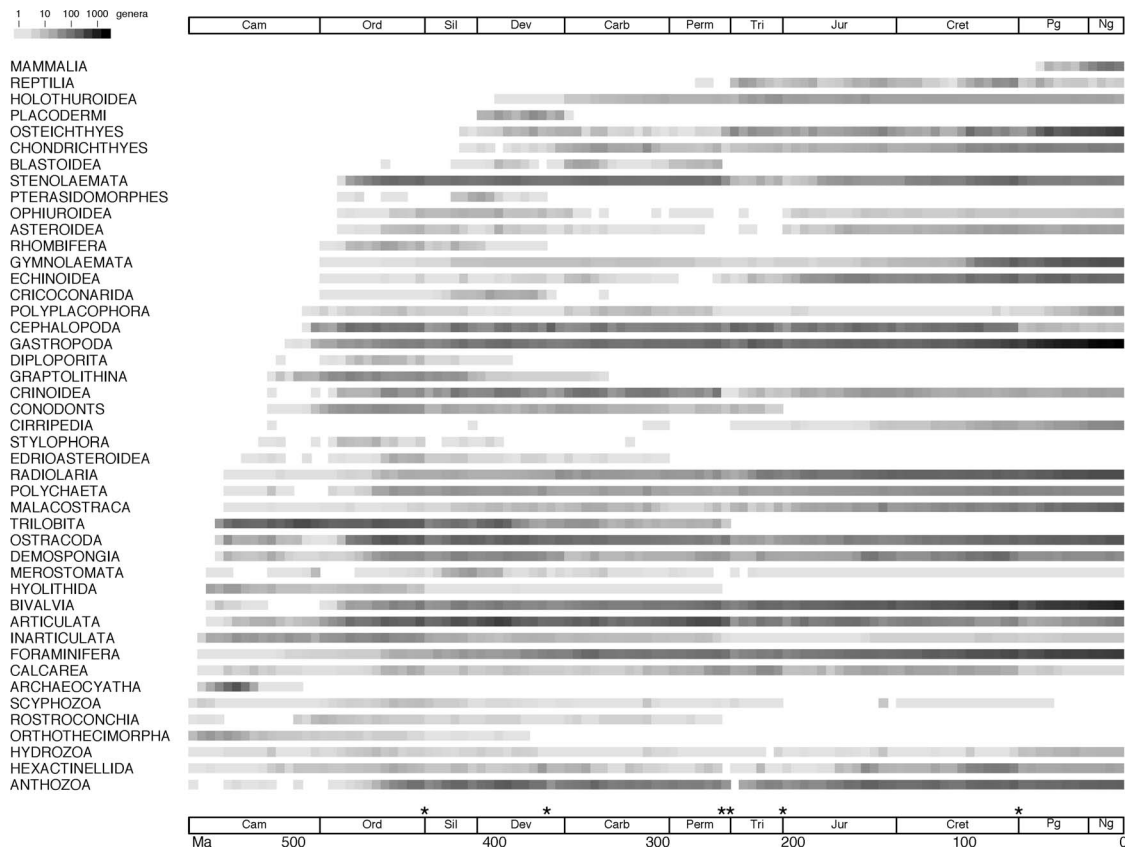
FIGURE 2. Diversity histories for 45 taxa from Sepkoski's genus compendium (2002), as compiled by Bambach (1999) and Bambach et al. (2004). Intensity of gray shading indicates diversity (genus richness). In our analyses, we omit Archaeocyatha, Blastoidea, Cricoconarida, Hyolithida, Mammalia, Orthothecimorpha, Pterasidomorphes, and Stylophora, because they have low diversities or short ranges. Timescale from Sepkoski (2002) uses 107 stages and substages. Mass extinctions are indicated by asterisks. Note that the x-axis scale is proportional to the number of substages in each period, not to time.

incompleteness, such as the Signor-Lipps effect. On this note, Foote (2007) presented an analysis of Sepkoski's data that suggested that the rates of extinction in many time intervals may be severe overestimates due to back-smearing, and others are subject to error terms of some magnitude as well. Ideally, we could run our analysis while taking these results into account, but this is not possible without class-level extinction and origination data.

We considered only classes with 40 or more genera, because smaller classes would have little effect on the analysis. We excluded a number of additional classes because they had a limited temporal range. These classes might have created analytical problems because some were extant predominantly in high-ex-

tinction substages, whereas others predominated in low-extinction substages. For instance, archaeocyathids had high diversity in the Cambrian, a time of elevated extinction rates, whereas mammals had high diversity in the Neogene, a time of diminished extinction rates. The presence of such combinations (analogous to collinearity in linear regression or confounded effects in analysis of variance) makes it difficult to estimate the class and substage coefficients (the κ_i and τ_t). To avoid such a possibility, we excluded the Archaeocyatha, Blastoidea, Cricoconarida, Hyolithida, Mammalia, Orthothecimorpha, Pterasidomorphes, and Stylophora. This left 37 classes with sufficiently long temporal ranges for the logistic regression algorithm to successfully distinguish class and substage effects (Fig. 2).

Because our data have not been standardized to account for sampling intensity, it is possible that our results are biased by variable and incomplete sampling, which could differentially affect classes with varying susceptibilities or substages with varying intrinsic severities. To account for such biases would be difficult and is beyond the scope of this paper.

Results

Table 3 gives the estimated τ_t coefficients for each substage, converted to probabilities, together with the observed (actual) extinction rates. The former values represent the extinction rate in each substage after adjusting for taxonomic susceptibility of the extant fauna. In other words, they estimate what the extinction rate would be if the distribution of classes were the same in each substage.

Figure 3A plots these adjusted extinction rates in each substage, together with the observed extinction rates. The adjusted rates (dashed gray line) are generally close to the observed extinction rates (solid black line). However, the observed rates exceed the adjusted rates for most of the Paleozoic, especially the Cambrian and Ordovician, implying that Paleozoic extinction levels were exacerbated by the higher susceptibility of classes then dominant (e.g., trilobites). Conversely, observed rates in the Cenozoic are lower than the adjusted rates, implying that extinction levels in that era were mitigated by the lower susceptibility of classes then dominant (e.g., gastropods and bivalves).

We can also assess the relationship between extinction rates before and after adjusting for taxonomic susceptibility by plotting adjusted versus observed extinction rates, with both axes on a log scale (Fig. 4). The relationship between adjusted and observed rates is similar for Paleozoic (open circles), Mesozoic (black circles), and Cenozoic (gray circles) substages, as indicated by points from the three eras lying approximately on parallel lines. The Cenozoic points are shifted higher by the adjustment for taxonomic susceptibility, indicating (as we saw previously) that Cenozoic extinction rates were tempered by the presence of extinction-resistant classes, causing our model to adjust observed rates upward. Conversely, the Paleozoic points are shifted lower, indicating that Paleozoic extinction rates were exacerbated by the presence of extinction-prone classes, causing our model to adjust observed rates downward.

For each of the three eras, the slope of the regression line (on the log-log scale) was statistically indistinguishable from 1. Note that a log-log model of the form $\log(Y) = a + b \log(X)$ implies that $Y = e^a X^b$ on an untransformed (non-log) scale, here with $b = 1$. It follows that on an untransformed scale, the adjusted rates are approximately equal to the observed rates multiplied by a constant, with values of the constant lowest for Paleozoic substages and highest for Cenozoic substages. Furthermore, the amount of spread around the regression line appears to be decreasing over time (Fig. 4). Thus not only is susceptibility decreasing over time (in agreement with Gilinsky's [1994] finding of decreasing volatility), but substage-to-substage variation in susceptibility appears to be decreasing as well.

Mass Extinctions.—Of particular interest are adjusted and observed extinction rates for the ''Big Five'' mass extinction events (Raup and Sepkoski 1982), with the end-Permian extinction considered to span two separate intervals, the Guadalupian and Djhulfian (Stanley and Yang 1994). Our adjustment for taxonomic susceptibility adjusts observed extinction rates downward for the two earliest mass extinctions and upward for the two latest mass extinctions (Table 3, Fig. 3). The adjustment least affects the two intervals for the end-Permian extinctions, which are intermediate in age. Judging by the observed rates in this data set, the Ordovician extinction was the second largest mass extinction, with 58% generic extinction, substantially more severe than the Cretaceous extinction with 47% extinction. The adjustment for taxonomic susceptibility, however, shows that the Ordovician, Guadalupian, Triassic, and Cretaceous events would have had nearly identical extinction severities (approximately 53%) if the distribution of classes had been identical.

Class Susceptibilities.—Table 4 gives the values of the susceptibility coefficients κ_i for each class, converted to probabilities (π_i) using

TABLE 3. Observed and adjusted extinction rates and taxonomic susceptibilities for each age or subage (henceforth referred to as ''substages'' as per common usage). Observed rates (Obs) are the raw overall percent extinction in each substage. Adjusted rates (Adj) (referred to as π_i in the text) are predicted by the logistic regression model given by equation (1), applied to data from the entire Phanerozoic. Susceptibility (Susc) is the taxonomic susceptibility of the classes extant in that substage. For instance, the observed (actual) extinction rate in the Wenlockian (Early Silurian) was 0.362, or 36.2%. After adjusting for taxonomic susceptibility, the logistic regression model predicts that a genus in an average class has a 0.296 probability (29.6%) of going extinct in the Wenlockian. This adjusted rate accounts for the taxonomic susceptibility of the fauna extant in that substage, and thus corrects for potential Simpson's paradox-type effects. The susceptibility of Wenlockian classes was 0.247 (24.7%). This quantity gives the expected extinction rate of the Wenlockian fauna if the intrinsic extinction severity in that substage were equal to that of an average Phanerozoic substage. In the Wenlockian, the logistic regression model adjusts the observed rate downward because fauna in that interval were relatively susceptible to extinction, thus exacerbating observed extinction rates. Data are from Sepkoski's genus compendium (2002), as compiled by Bambach (1999) and Bambach et al. (2004). Period abbreviations: Ng, Neogene; Pg, Paleogene; K, Cretaceous; J, Jurassic; Tr, Triassic; P, Permian; Pn, Pennsylvanian; M, Mississippian; D, Devonian; S, Silurian; O, Ordovician; C, Cambrian. Mass extinction stages are boldfaced.

| Per.	Substage	Obs.	Adj.	Susc.	Per.	Substage	Obs.	Adj.	Susc.
Ng	Pliocene	0.088	0.104	0.159	Pn	Moscovian-l	0.200	0.181	0.206
Ng	Miocene-l	0.071	0.084	0.158	Pn	Moscovian-e	0.087	0.070	0.211
Ng	Miocene-m	0.085	0.102	0.155	Pn	Bashkirian-l	0.094	0.077	0.209
Ng	Miocene-e	0.063	0.077	0.155	Pn	Bashkirian-e	0.101	0.080	0.213
Pg	Oligocene-l	0.040	0.047	0.156	M	Serpukhovian-l	0.070	0.060	0.197
Pg	Oligocene-e	0.072	0.086	0.157	M	Serpukhovian-e	0.297	0.265	0.221
Pg	Eocene-l	0.156	0.189	0.155	M	Visean-l	0.322	0.283	0.226
Pg	Eocene-m-l	0.054	0.066	0.154	M	Visean-e	0.239	0.214	0.213
Pg	Eocene-m-e	0.102	0.118	0.160	M	Tournaisian-l	0.176	0.147	0.219
Pg	Eocene-e	0.075	0.088	0.158	M	Tournaisian-e	0.208	0.181	0.214
Pg	Thanetian	0.099	0.121	0.153	D	Famennian-l	0.317	0.286	0.221
Pg	Danian	0.115	0.143	0.151	D	Famennian-e	0.283	0.214	0.257
K	**Maastrichtian**	**0.471**	**0.528**	**0.169**	**D**	**Frasnian-l**	**0.364**	**0.332**	**0.222**
K	Campanian-l	0.114	0.121	0.173	D	Frasnian-e	0.271	0.210	0.245
K	Campanian-e	0.094	0.099	0.172	D	Givetian-l	0.284	0.240	0.229
K	Santonian	0.087	0.090	0.175	D	Givetian-e	0.247	0.206	0.226
K	Turonian-Coniacian	0.129	0.125	0.186	D	Eifelian	0.373	0.301	0.251
K	Cenomanian	0.248	0.254	0.188	D	Emsian	0.359	0.276	0.259
K	Albian-l	0.123	0.119	0.184	D	Siegenian	0.190	0.141	0.243
K	Albian-m	0.046	0.044	0.179	D	Gedinnian	0.248	0.195	0.239
K	Albian-e	0.068	0.064	0.180	S	Pridolian	0.234	0.191	0.228
K	Aptian	0.186	0.190	0.184	S	Ludlovian	0.393	0.338	0.240
K	Barremian	0.101	0.098	0.184	S	Wenlockian	0.362	0.296	0.247
K	Hauterivian	0.087	0.085	0.183	S	Llandoverian-l	0.159	0.126	0.227
K	Valanginian	0.111	0.109	0.184	S	Llandoverian-m	0.139	0.109	0.225
K	Berriasian	0.087	0.085	0.182	S	Llandoverian-e	0.115	0.095	0.216
J	Tithonian-l	0.214	0.210	0.192	**O**	**Ashgillian-l**	**0.575**	**0.533**	**0.241**
J	Tithonian-e	0.137	0.131	0.190	O	Ashgillian-e	0.118	0.086	0.238
J	Kimmeridgian	0.187	0.175	0.198	O	Caradocian-l	0.164	0.124	0.236
J	Oxfordian	0.195	0.182	0.201	O	Caradocian-m	0.230	0.181	0.235
J	Callovian	0.203	0.175	0.214	O	Caradocian-e	0.220	0.168	0.242
J	Bathonian	0.179	0.164	0.202	O	Llandeilian	0.198	0.137	0.256
J	Bajocian-l	0.128	0.118	0.195	O	Llanvirnian-l	0.129	0.081	0.263
J	Bajocian-e	0.112	0.097	0.199	O	Llanvirnian-e	0.268	0.179	0.274
J	Aalenian	0.069	0.062	0.192	O	Arenigian-l	0.335	0.225	0.286
J	Toarcian	0.217	0.192	0.211	O	Arenigian-e	0.361	0.246	0.285
J	Pliensbachian	0.255	0.239	0.204	O	Tremadocian-l	0.432	0.335	0.270
J	Sinemurian	0.156	0.135	0.206	O	Tremadocian-e	0.494	0.379	0.282
J	Hettangian	0.087	0.082	0.180	C	Trempealeauan	0.603	0.458	0.314
Tr	**Norian-l**	**0.490**	**0.537**	**0.186**	C	Franconian	0.631	0.487	0.303
Tr	Norian-e	0.279	0.260	0.213	C	Dresbachian	0.682	0.562	0.297
Tr	Carnian	0.391	0.374	0.220	C	Late Middle-l	0.502	0.379	0.285
Tr	Ladinian	0.279	0.258	0.213	C	Late Middle-e	0.504	0.393	0.275
Tr	Anisian	0.301	0.243	0.247	C	Middle Middle	0.590	0.500	0.266
Tr	Induan	0.455	0.374	0.274	C	Early Middle	0.367	0.272	0.267
P	**Djhulfian**	**0.696**	**0.709**	**0.211**	C	Toyonian	0.434	0.341	0.265
P	**Guadalupian**	**0.549**	**0.531**	**0.225**	C	Botomian-l	0.436	0.340	0.267
P	Leonardian-l	0.227	0.190	0.224	C	Botomian-e	0.544	0.462	0.260
P	Leonardian-e	0.200	0.167	0.222	C	Atdabanian-l	0.498	0.444	0.236
P	Sakmarian-l	0.133	0.106	0.221	C	Atdabanian-e	0.476	0.454	0.212
P	Sakmarian-e	0.066	0.051	0.216	C	Tommotian-l	0.432	0.555	0.129
P	Asselian	0.102	0.081	0.217	C	Tommotian-e	0.197	0.236	0.137
Pn	Stephanian-l	0.153	0.127	0.216	C	Nemakit-Daldynian	0.353	0.384	0.162
Pn	Stephanian-e	0.104	0.082	0.216					
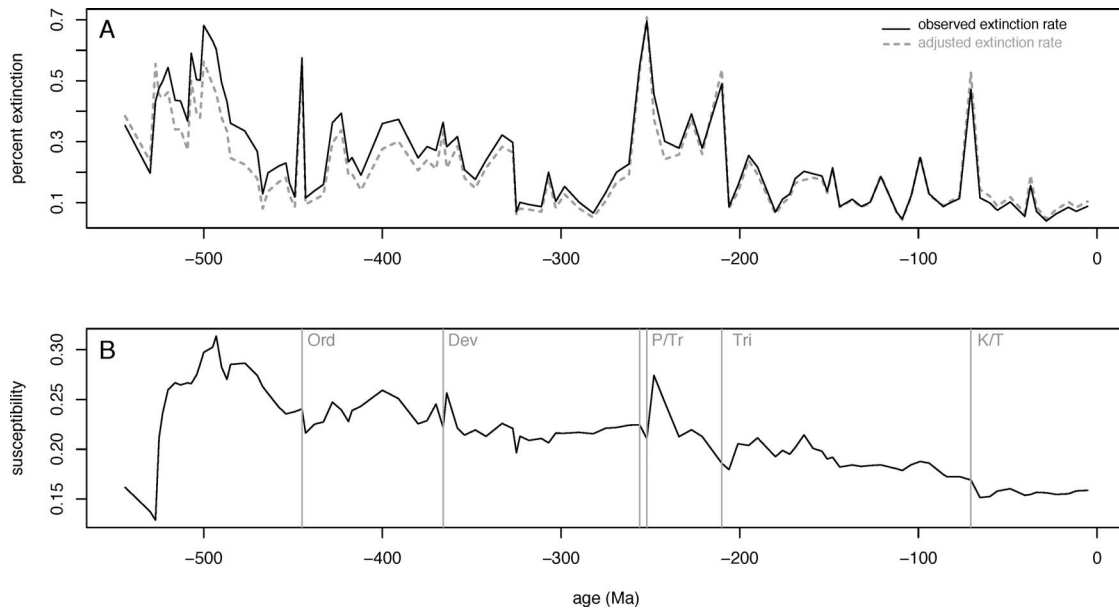
FIGURE 3. A, Time series plot of observed (solid black line) and adjusted (dashed gray line) extinction rates at the genus level, from Table 3. Adjusted rates account for variations in taxonomic susceptibility in different substages and are calculated by using the logistic regression model given by equation (1). Observed rates in the Paleozoic are generally adjusted downward, indicating that substages in this era had extinction-prone fauna, and observed Paleozoic extinction rates were exacerbated by high taxonomic susceptibility. In contrast, observed rates in the Cenozoic are generally adjusted upward, indicating that substages in this era had extinction-resistant fauna, and observed Cenozoic extinction rates were mitigated by low taxonomic susceptibility. B, Taxonomic susceptibility of the fauna in each substage, calculated by using the coefficients in Table 4 weighted by the diversity of each class. Mass extinctions are marked by vertical gray lines. A long-term decline in susceptibility is evident, which explains 29% of the Phanerozoic decline in observed extinction rates (see text for details). Note the spike in taxonomic susceptibility after the end-Permian mass extinction.

equation (1). These values represent the extinction rate of each class in an average Phanerozoic substage. We emphasize that these values are not simply the observed average extinction rates for each class, because these susceptibility coefficients adjust for variation in diversity within each class over time. For instance, suppose two classes have exactly the same intrinsic extinction susceptibility, but one class attains its highest diversity during the early Paleozoic, whereas the other attains its highest diversity during the Cenozoic. The first class will have a higher observed extinction rate than the second because it is extant predominantly during a time of higher intrinsic extinction severity, whereas the second is extant predominantly during a time of lower intrinsic extinction severity. Thus the first class will artificially appear more extinction-prone and the second more extinction-resistant, even though in fact they have the same intrinsic susceptibility. The values in Table 4

adjust for this bias. (Note that these rates can still be affected by taxonomic practice; for example, oversplit taxa may appear to have artificially high extinction rates. However, this is unavoidable in any analysis of this type.)

Using these adjusted class extinction rates, we calculated the susceptibility of the fauna as a whole in each Phanerozoic substage. For each substage, we multiplied the adjusted extinction rate for each class by the number of genera in that class. The sum of these products is an estimate of the total number of genera that would have gone extinct in that substage if it had had an average extinction severity. Dividing this sum by the diversity in the substage yields an adjusted extinction rate. We thus infer the taxonomic susceptibility of the fauna in each substage (Fig. 3B). In other words, these values estimate what the extinction rate for each substage would have been if all substages had experienced a constant extinction trigger, and therefore all variation in
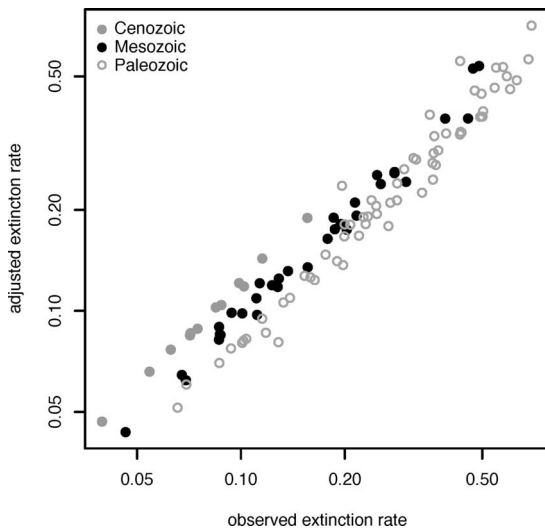
FIGURE 4. Plot of adjusted versus observed extinction rates (Table 1, Fig. 3). On a log-log scale, regression lines for each era (not shown for clarity) have slopes statistically indistinguishable from 1.0 but different intercepts. The regression line for Cenozoic substages has the highest intercept, indicating that extinction rates for these stages are adjusted upward when controlling for taxonomic susceptibility. The regression line for Paleozoic substages has the lowest intercept, indicating that extinction rates for these stages are adjusted downward when controlling for taxonomic susceptibility. See also Figure 3 caption.

observed extinction rates resulted from differences in taxonomic composition.

There is a natural correspondence between the top and bottom panels of Figure 3. The adjusted extinction rate falls below the observed rate in Figure 3A when taxonomic susceptibility is relatively high in Figure 3B. During such times, extinction rates were exacerbated

by a predominance of susceptible classes, rather than being driven solely by an intrinsically severe trigger. Therefore, the logistic regression adjusts the observed rate downward to account for this elevated faunal susceptibility. Conversely, the adjusted extinction rate exceeds the observed rate in Figure 3A when susceptibility is relatively low in Figure 3B. At such times, the severity of the intrinsic extinction trigger is mitigated by the resistance to extinction of the extant fauna. Therefore, the logistic regression adjusts the observed rates upward to account for this low susceptibility. Finally, in substages in which the adjusted and observed rates are equal or nearly so, as is the case during the Cretaceous, extant classes have a combined susceptibility close to the Phanerozoic average.

Statistical Significance.—A natural question is whether our model adjusting for taxonomic susceptibility is a significant improvement over a model without such an adjustment. This is equivalent to asking whether classes differ significantly in susceptibility. To assess statistical significance, we compared the following two logistic regression models:

(a) a null model that omits the coefficients for class susceptibility, given by the equation $\pi_{it} = 1/\{1 + \exp[-(\beta + \tau_t)]\}$ [cf. eq. 1]. According to this null model, the probability that a genus in class i goes extinct in substage t depends only on the identity of substage t and not on the identity of class i. In other words, the overall extinction

TABLE 4. Class susceptibilities from the logistic regression model given by equation (1), applied to data from the entire Phanerozoic and expressed on a probability scale (π_i). For instance, a genus in class Holothuroidea has a 0.05 probability of going extinct in an average Phanerozoic substage, whereas a genus in class Placodermi has a 0.60 probability of going extinct in an average Phanerozoic substage. These values account for the intrinsic severity of the substages in which each class was extant, and thus correct for potential Simpson's paradox-type effects. Data are from Sepkoski's genus compendium (2002), as compiled by Bambach (1999) and Bambach et al. (2004).

Class	π_i	Class	π_i	Class	π_i	Class	π_i
Holothuroidea	0.05	Calcarea	0.13	Ostracoda	0.18	Merostomata	0.30
Radiolaria	0.06	Gastropoda	0.13	Chondrichthyes	0.19	Crinoidea	0.31
Polychaeta	0.06	Polyplacophora	0.14	Conodonts	0.22	Articulata	0.33
Cirripedia	0.09	Inarticulata	0.14	Echinoidea	0.22	Rhombifera	0.34
Stenolaemata	0.11	Bivalvia	0.14	Hexactinellida	0.23	Trilobita	0.34
Gymnolaemata	0.12	Foraminifera	0.15	Anthozoa	0.23	Diploporita	0.35
Rostroconchia	0.12	Asteroidea	0.16	Edrioasteroidea	0.24	Rhombifera	
Hydrozoa	0.12	Demospongia	0.17	Graptolithina	0.24	Reptilia	0.48
Ophiuroidea	0.12	Malacostraca	0.17	Osteichthyes	0.28	Cephalopoda	0.53
Scyphozoa	0.13					Placodermi	0.60

rate in a substage depends only on the intrinsic extinction severity of that substage, not on the susceptibility of the fauna extant in that substage; and

(b) our full model (including the coefficients for class susceptibility) as given by equation (1).

For each model, we calculated the residual deviance, a standard likelihood-based measure of fit that is analogous to the sum of squared residuals in linear regression (Hosmer and Lemeshow 2000). For a given data set, smaller residual deviance indicates better fit. The residual deviance was 19,757 on 2884 degrees of freedom for the null model, and 11,329 on 2847 degrees of freedom for the full model, so the full model does explain the data better, but is this difference statistically significant?

To answer this question, we test the null hypothesis that class susceptibility is not a significant predictor of extinction rate (i.e., that the class susceptibility coefficients are all zero) by using a likelihood ratio test (Casella and Berger 2002; see Wang and Everson 2007 for a brief introduction). The test statistic is the difference between the residual deviances of the null model and the full model, which here equals $19,757 - 11,329 = 8428$. Under the null hypothesis, this test statistic has a chi-square distribution, with degrees of freedom equal to the difference between the degrees of freedom of the null model and the full model (here, $2884 - 2847 = 37$). The p-value is the probability that a chi-square random variable with 37 degrees of freedom would exceed a value of 8428, a probability that is virtually zero. Thus we reject the null hypothesis and conclude that class susceptibility is a statistically significant predictor of extinction rate. In other words, our full model (b) adjusting for taxonomic susceptibility is significantly different from (and better than) the null model (a) lacking such an adjustment.

In Figure 3A, the adjusted and observed extinction rates appear fairly similar over much of the Phanerozoic. It is natural to ask whether these rates are significantly different. We can use the comparison between the full and null models to answer this question. The adjusted

rates are the predicted values from the full model (b). The observed rates are the predicted values from the null model (a), because the null model does not account for class susceptibility and its predicted values therefore simply reproduce the observed rates in each substage. Therefore, the fact that the full model is significantly different from the null model implies that the adjusted rates (taken as a whole, not just in any particular substage) are significantly different from the observed rates.

Alternatively, we can compare the null and full models using Akaike's Information Criterion (AIC) (Akaike 1974; see Hunt 2006 for a paleontological application). AIC is a likelihood-based method for choosing among candidate models, taking into account the parsimoniousness (number of parameters) of each model. The best model among the candidate models is the one with the smallest AIC. Here the null model has an AIC of 26,020 and the full model an AIC of 17,666, so we see again that the latter model (incorporating class susceptibility) is preferred.

Decline in Phanerozoic Extinction Rates

Many authors have noted a decline in extinction rates over the Phanerozoic. Reasons proposed to explain this decline include an increase in fitness (Raup and Sepkoski 1982), an increase in the number of species per genus (Flessa and Jablonski 1985), an aging fauna (Boyajian 1986), sampling bias (Pease 1992), sorting of higher taxa (Stanley 1979, 2007; Sepkoski 1984, 1991; Van Valen 1985, 1987; Gilinsky 1994), and changes in community structure (Roopnarine et al. 2007). (Bambach et al. [2004] suggested that extinction history consisted of several phases of high and low rates rather than a steady decline.) Our analysis shows that taxonomic susceptibility (at the class level) has declined (Fig. 3B), so part of the Phanerozoic decline in extinction rates can be attributed to this factor. However, our adjusted extinction rates after adjusting for taxonomic susceptibility (Fig. 3A) also decline; thus part of the Phanerozoic decline can be also attributed to factors not accounted for by our model. For example, a decline in total extinction rates that resulted from declines in rates *within* higher taxa rather than shifts in

dominance *among* higher taxa would not show up in this model as a decline in susceptibility (e.g., Stanley 2007: p. 45). A linear regression fit to the observed extinction rates gives a slope of -0.000602 (i.e., a decline of -0.06 percentage points per million years). Over the entire Phanerozoic, this rate of change translates to a drop of 0.327 (32.7 percentage points). A linear regression fit to the adjusted extinction rates gives a slope of -0.000427 (i.e., a decline of -0.04 percentage points per million years). Over the entire Phanerozoic, this rate of change translates to a drop of 0.232 (23.2 percentage points). Thus we estimate that changes in taxonomic susceptibility at the class level are responsible for 29% of the Phanerozoic decline in extinction rates ($=(32.7 - 23.2)/32.7$), with other factors responsible for the remaining 71%.

Background versus Mass Extinction: Different Selective Regimes?

Many authors have studied whether mass extinctions are the right tail of a continuous distribution of extinction events, or whether they are a qualitatively different phenomenon from background extinction (Raup and Sepkoski 1982; Jablonski 1986; Benton 1995; Miller 1998; Wang 2003; Bambach et al. 2004; Jablonski 2005; Foote 2007). To investigate this question, we calculated the susceptibility coefficients κ_i for each class by fitting the logistic regression model to two different data sets: first, data from only the Big Five mass extinction substages, and second, data from only background extinction substages. If background and mass extinctions have similar selectivity, we would expect these two sets of susceptibility coefficients to be highly correlated. On the other hand, if background and mass extinctions differ in selectivity, we would expect these two sets of susceptibility coefficients to show little correlation. In fact, classes that have high susceptibility in background substages also tend to have high susceptibility during mass extinctions (Fig. 5; $r = 0.89$).

Assessing Model Fit

In this section, we assess whether our logistic regression model adequately fits the data. To be of practical value, all statistical models
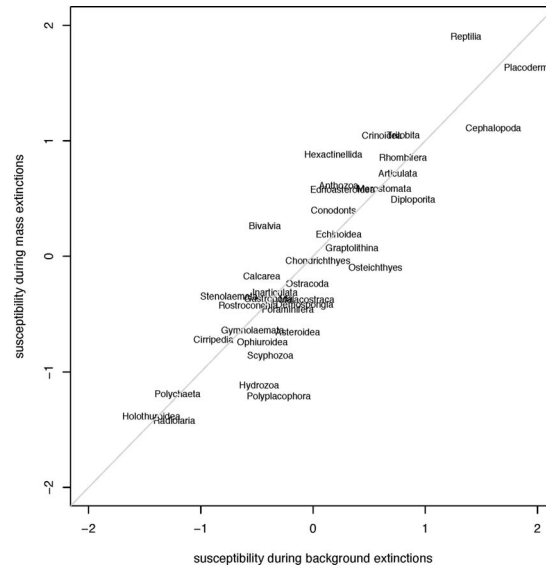

FIGURE 5. Comparison of class susceptibility coefficients (κ_i) estimated only from mass extinction substages and only from background extinction substages. Gray line is the line $y = x$. There is a strong correlation ($r = 0.89$) between class susceptibilities in mass extinctions and background extinctions, implying that there is continuity of effect between these phenomena and arguing against distinct selective regimes at the class level.

must make simplifying assumptions about the structure of the data being modeled. As discussed earlier, our model assumes that the effect of each class and each substage on extinction rates is additive, with no interaction between the two. In other words, the model assumes that the effect of any particular substage is the same for all classes, and the effect of any particular class is the same in all substages. In addition, our model accounts for the susceptibility of each class only through a coefficient (κ_i) that reflects its susceptibility in an average Phanerozoic substage. If the susceptibility of a class systematically varies over time, using only the average Phanerozoic susceptibility may not adequately explain observed extinction patterns.

To determine whether our logistic regression model adequately captures the class and substage dynamics seen in the data set, we first compared the observed extinction rate to the total extinction rate (aggregated over all classes) predicted by the model (i.e., π_{ij} in eq. 1). There was a very close correspondence between these two quantities over the 107 Phan-
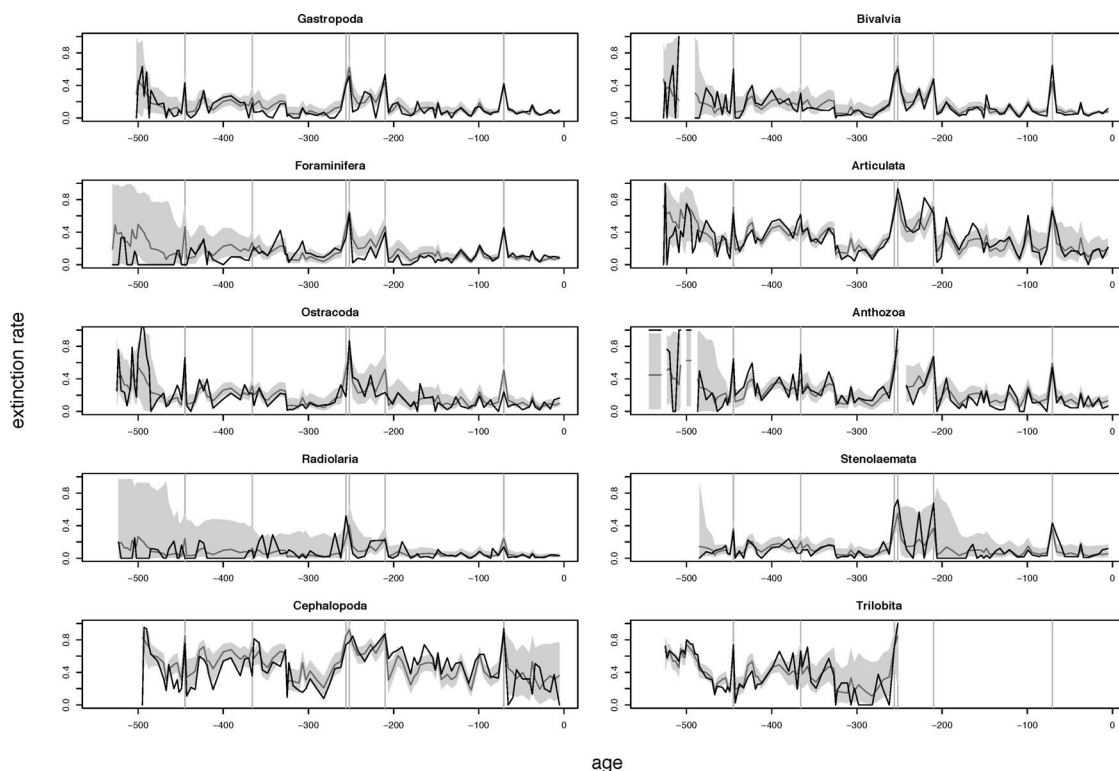
FIGURE 6. Comparison of observed (black) and predicted (gray) extinction rates for each of the ten classes having the highest cumulative diversity over the Phanerozoic. Although some discrepancies are evident, there is generally a fairly close match between observed and predicted rates. See text for discussion. Predicted extinction rates (π_{ij}) in each substage were calculated by using equation (1). Gray shaded regions indicate 95% prediction intervals, which account for variability due to two sources: (1) variability in the predicted extinction rates, given by the standard error of the predicted π_{ij}, and (2) binomial sampling variability in the observed extinction rates, given by the standard error of the observed rates. The margin of error for the prediction interval is twice the square root of the sum of squares of these two standard errors.

erozoic stages and substages; the correlation coefficient was 0.9998 for the raw data and 0.9997 for first differences. Although this correspondence is encouraging, it is necessary to compare observed and predicted extinction rates for individual classes (Fig. 6), because the match for aggregated extinction rates could mask discrepancies at finer taxonomic levels. For each of the ten classes having the highest cumulative diversity over the Phanerozoic, we calculated the predicted extinction rates in each substage using equation (1). In each plot, the black line gives the observed extinction rate, and the gray line the predicted rate (i.e., the extinction rate π_{ij} estimated by the logistic regression model). In order to visually assess whether the observed and predicted rates match, we display 95% prediction intervals (gray shaded regions). These error

bars account for uncertainty due to two sources: (1) the predicted extinction rate may differ from the true extinction rate if the logistic regression does not accurately model extinction dynamics, and (2) the observed extinction rate may differ from the true extinction rate because of random sampling variability, particularly when sample sizes are small. If the model accurately reflects true extinction rates, then most observed rates should lie within the 95% prediction intervals.

In general, the predicted and observed rates match fairly well. Some discrepancies are visible when diversity is low. For example, predicted rates are too high for Foraminifera in the early Paleozoic. A similar pattern can be seen for Radiolaria in the Devonian and Stenolaemata in the Jurassic. However, in these cases the prediction intervals are very wide

because diversity is low (e.g., foraminiferan diversity does not exceed six genera until the lower Caradocian). As observed rates still mostly fall within the prediction intervals, these discrepancies are likely to indicate random fluctuations due to small sample size, rather than systematic problems in the model.

Other discrepancies do not appear to be due to small-sample-size variability. Cephalopods have lower rates of extinction than predicted in the Paleozoic and higher in the Jurassic and Cretaceous. This difference may relate to the dominance in the Jurassic and Cretaceous of ammonites, which had high rates of turnover and may be oversplit taxonomically because of their biostratigraphic utility. As another example, foraminifera have higher rates of extinction than expected in the Carboniferous, Permian, and Cenozoic, when they are likewise used for biostratigraphy. In these cases, the misfit between the model and the observed data may result from combining groups (e.g., ammonites and ammonoids) with different diversity dynamics; separating these groups might improve the fit of the model. In general, however, the predicted rates are a good match for the observed rates, especially for gastropods and bivalves, the two most diverse classes.

Of particular interest are the predicted extinction rates for mass extinction events and recovery intervals, as those substages are the ones in which we might expect the assumption of additivity to be most likely violated because of unusual extinction triggers and potentially uniquely selective extinctions. Some discrepancies can be seen in Figure 6: foraminifera have lower extinction rates in the Ordovician extinction and in the post-Permian recovery, compared to the model predictions; ostracodes have lower extinction rates in the Triassic and the Cretaceous extinctions; cephalopods have lower extinction rates in the post-Ordovician and post-Cretaceous recoveries and higher in the post-Triassic recovery; and stenolaemate bryozoans have higher extinction rates in the Triassic extinction. In general, however, the predicted and observed rates match well in mass extinction and recovery intervals.

In summary, although there are occasional discrepancies among taxa and intervals, the logistic regression model seems to do a good job of modeling extinction dynamics despite its simplifying assumption that the effects of each class and each substage are additive.

Mass Extinctions and Their Recoveries

Do mass extinctions occur during times of relatively high taxonomic susceptibility, or do they occur despite low susceptibility? In Figure 3B, we see that mass extinctions do not typically occur when the extant fauna are particularly susceptible. On the contrary, the Devonian, Triassic, and Cretaceous extinctions were preceded by a decrease in susceptibility. The Ordovician extinction was preceded by a slight increase in susceptibility, but susceptibility was still low compared to the previous 75 Myr. Similarly, the penultimate substage of the Permian (the Guadalupian) was preceded by a slight increase in susceptibility, but susceptibility had remained essentially steady since the end of the Devonian 100 Myr earlier. From the Guadalupian to the final Permian stage (the Djhulfian) there was a decrease in susceptibility, presumably associated with the Guadalupian extinctions.

Using computer simulations of Karoo Basin food webs, Roopnarine et al. (2007) suggested that Late Permian terrestrial communities were not particularly susceptible but Early Triassic recovery communities were unstable, implying that the Permian extinction disturbed the stability of trophic networks. We find a similar effect here, although our conclusions are global in scope rather than at the community level. These findings are consistent with other work concluding that post-extinction fauna were depauperate or impoverished (Schubert and Bottjer 1995; Rodland and Bottjer 2001; Twitchett et al. 2001; Pruss and Bottjer 2004a; Chen et al. 2005; Payne 2005; Erwin 2006; Payne et al. 2006). Our analysis shows that susceptibility in the final Permian stage (the Djhulfian) was at its lowest level of the preceding 50 Myr (Fig. 3B). Immediately after the end-Permian extinction, however, susceptibility increased sharply in the first stage of the Triassic (the Induan). This spike is largely due to an increase in diversity of cephalopods (Fig. 7A), the second most sus-

ceptible class (Table 4), and is in fact the most dramatic shift in susceptibility of the Phanerozoic after the Early Cambrian. In fact, cephalopods increased from 5.6% of genera in the database in the latest Permian substage to 27% of genera in the earliest Triassic substage. This was not just an increase in relative terms compared to other genera decimated by the extinction, but an absolute increase in the number of genera: cephalopods increased from 48 to 163 genera while total diversity dropped from 866 to 603 genera.

Is such a pattern a general feature of mass extinctions and their recovery intervals? A similar pattern can be seen in the Late Cambrian. Although not considered among the Big Five mass extinctions, the Middle and Late Cambrian were times of elevated extinction rates (Bambach 2006). Shortly after Cambrian extinction rates peak in the Dresbachian, a spike in susceptibility occurs in the Trempealeauan (490–493 Ma) (Fig. 3B). Although not as dramatic a change as the Early Triassic increase in susceptibility, this spike represents the highest level of susceptibility of the entire Phanerozoic. This is again primarily due to cephalopods, which undergo their initial diversification from 1 to 42 genera. The Devonian (Frasnian/Famennian) extinction follows this pattern as well, although it is less pronounced. Susceptibility in the late Frasnian is locally low but rises in the early Famennian, again coinciding with a diversification of cephalopods from 53 to 177 genera. The Triassic extinction follows a generally similar pattern. Susceptibility declines throughout most of the Triassic, and continues to do so in the Hettangian after the extinction; the rise in susceptibility is delayed until the succeeding Sinemurian stage. This rise is due primarily to an increase in cephalopod genera from 30 to 84.

Not all mass extinctions follow this pattern of increasing susceptibility in recovery intervals. Susceptibility drops in the early Llandoverian immediately after the Ordovician extinction, coinciding with a relative decrease in many high-susceptibility classes (Cephalopoda, Trilobita) and a relative increase in some low-susceptibility classes (Foraminifera, Gastropoda, Polychaeta, Radiolaria, Stenolaema-

ta). A similar decrease in susceptibility is seen in the Danian immediately after the Cretaceous extinction, coinciding with a relative decrease in some high-susceptibility taxa (Cephalopoda, Reptilia) and an increase in some low-susceptibility taxa (Gastropoda, Radiolaria), although the low-susceptibility Bivalvia declined as well.

In summary, there does not seem to be a general pattern of mass extinctions occurring during times of high susceptibility. Nor does there seem to be a consistent pattern of susceptibility change at mass extinction events and their recovery intervals. Observed patterns appear to depend on the particular taxa that survive and radiate following an extinction, which vary from event to event. Thus mass extinctions appear to lack a common effect, suggesting that they do not share a common cause.

Evenness and Susceptibility

On ecological time scales, biodiversity can enhance the stability of ecosystems (Tilman and Downing 1994; McGrady-Steed et al. 1997; Naeem and Li 1997; McCann 2000), and Kiessling (2005) found that high diversity in reefs enhanced stability on million-year time scales as well. Given these findings, we tested for a similar effect of taxonomic composition on global extinction rates: perhaps global faunas containing a wide range of higher taxa are typically resistant to extinction, whereas faunas containing few higher taxa are susceptible to extinction. (Although stability is presumably enhanced by diversity at local rather than global levels, there may nonetheless be an effect if local and global diversity are related [e.g., Sepkoski et al. 1981].) We measured the diversity of higher taxa within each substage by the evenness of generic diversity within classes, quantified using PIE (Olszewski 2004), transformed to $1/(1 - \text{PIE})$ to improve symmetry. Substages containing many common higher taxa have high evenness; those dominated by relatively few taxa have low evenness.

We compared evenness at the class level with adjusted extinction rates (comparing evenness with observed extinction rates gave similar results). This analysis differs from
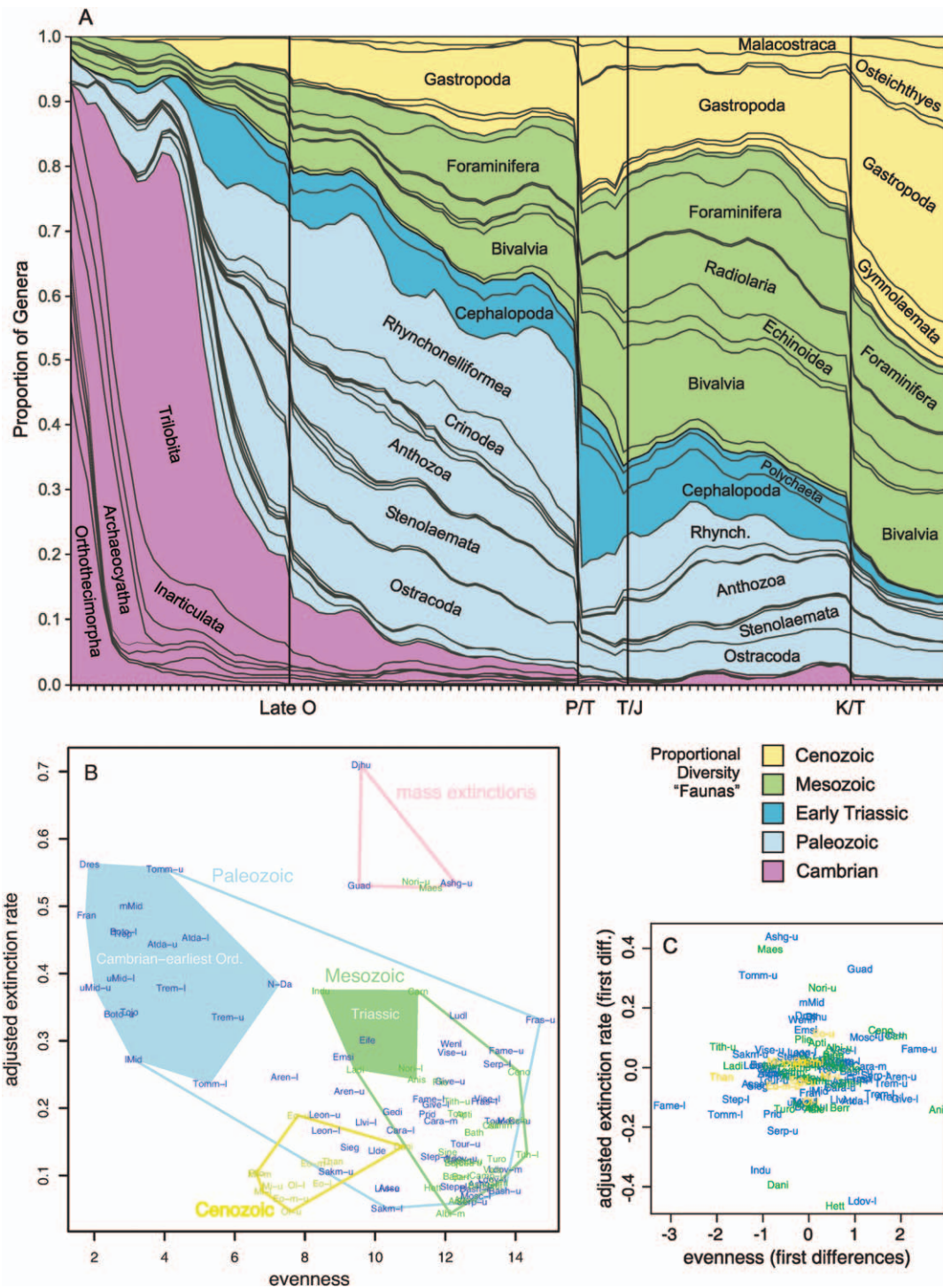
FIGURE 7.   Relationships between evenness of genera within classes and extinction rate. A, Proportional genus di-
versity of classes in Sepkoski's compilation. To reduce noise, values are smoothed with a five-bin running average,
except across the marked mass extinctions. Classes are ordered and grouped according to their stage or substage
of maximum proportional diversity. B, Adjusted extinction rate versus evenness, here measured as $1/(1 - \text{PIE})$.
Adjusted extinction rates are inversely correlated with evenness ($r = -0.49$ for all substages; $r = -0.64$ when the
cluster of mass extinction intervals [pink region in upper right] is excluded). The negative correlation holds when the
Paleozoic ($r = -0.78$) and Mesozoic ($r = -0.55$) are considered separately, but not in the Cenozoic ($r = 0.41$).

those above because here extinction rate is compared with a measure of the diversity of taxa present in an interval, regardless of the identity of those taxa, whereas the previous analyses adjusted extinction rates on the basis of the identities of taxa present.

As hypothesized, adjusted extinction rates are inversely correlated with evenness (Fig. 7B; $r = -0.49$ for all substages). The correlation increases when the cluster of mass extinction intervals in the upper right is excluded ($r = -0.64$ for background intervals only). If we consider each era separately, we find an inverse correlation in both the Paleozoic ($r = -0.78$) and Mesozoic ($r = -0.55$), with a decline in extinction and increase in evenness from the Triassic to the later Mesozoic paralleling the trends from the Cambrian–earliest Ordovician to the later Paleozoic. However, the correlation within the Cenozoic substages is lower and positive ($r = 0.41$): the Danian (earliest Paleocene) is most similar to Mesozoic values, and evenness then actually decreases through time as gastropods radiate and make up a larger proportion of the fauna (Fig. 7A). In the upper right, the cluster of mass extinction outliers includes the Guadalupian (Stanley and Yang 1994) and the traditional ''Big Five'' (Raup and Sepkoski 1982) except for the upper Frasnian, which Bambach et al. (2004) labeled a ''mass depletion'' of diversity but not an interval having especially elevated extinction relative to adjacent Devonian intervals.

The inverse correlation between evenness and extinction and the parallel temporal trends in these variables in the Paleozoic and Mesozoic suggest that a causal relationship is worth investigating, but further analysis does not support such a link. When we take first differences of both adjusted extinction rate and evenness, the correlation disappears (Fig. 7C; $r = -0.001$). Apparently, evenness is not a direct cause of high global extinction; rather,

both are responses to other variables. Note that substages with low evenness (below 6.0) are confined to the Cambrian and Early Ordovician. It is thus difficult to determine whether the high adjusted extinction rates of these substages are a result of low evenness, or of other conditions specific to the Cambrian and Early Ordovician. We emphasize that the high adjusted extinction rates in these intervals are not caused by a relative abundance of susceptible taxa (e.g., trilobites); the effects of susceptibility have already been accounted for in these adjusted rates. That is, these high adjusted rates are due to within-class trends rather than sorting among classes. This can be seen in Figure 4C of Bambach et al. (2004), which shows that extinction rates for both trilobites and non-trilobite taxa decline during or immediately after the Early Ordovician.

The similarity between the Cambrian-earliest Ordovician and the Triassic in Figure 7B is noteworthy. For both sets of substages, the points lie in the upper left of the region occupied by the corresponding era. That is, Cambrian-earliest Ordovician substages are the Paleozoic intervals with the highest adjusted extinction rate and lowest evenness, and the same holds for Triassic substages among Mesozoic intervals. Several causes have been suggested for high rates of taxonomic turnover in the Cambrian and Early Ordovician: functional limitations of early animals that made them more vulnerable to extinction (Bambach et al. 2002), low diversity or low ecospace occupation in the early Paleozoic oceans (Bambach 1983, 1985; Bambach et al. 2002, 2004), or physical stresses, such as may be indicated by carbon isotopes (Brasier and Sukhov 1998; Saltzman et al. 2000). Some of these factors could apply as well to the Early Triassic, when the end-Permian extinction had devastated marine communities. Diversity was as low as it had been since the Ordovician Radiation, both within habitats and

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The Cambrian–earliest Ordovician can be seen to be similar to the Triassic when each is compared to its own era. Substages decline in extinction rate and increase in evenness from the Cambrian and earliest Ordovician to later Paleozoic times (blue), and Mesozoic values trend similarly from the Triassic to the later Mesozoic (green). Evenness then decreases through the Cenozoic as gastropods radiate (yellow). C, No correlation is apparent when first differences are taken, making a causal relationship unlikely.

globally (Bambach 1977; Sepkoski 1987). Ecospace occupation was dramatically reduced by the end-Permian extinction—for example, in tiering above and below the sediment-water interface (Ausich and Bottjer 1982; Pruss and Bottjer 2004a; Twitchett et al. 2004). Large carbon isotope excursions characterize the series (Payne et al. 2004), and the environment may have been unstable or hazardous in a number of ways (e.g., Isozaki 1997; Retallack 1999; Wignall and Twitchett 2002). Metazoan communities were so disrupted that microbialites became prominent (Schubert and Bottjer 1992; Lehrmann et al. 2003; Pruss and Bottjer 2004b), as they had been in the Cambrian, and other microbially influenced sedimentary structures became more common (Pruss et al. 2004). As the world's oceans recovered from the Permian extinction, all of these factors returned to ''normal,'' and taxonomic evenness increased and extinction rate declined.

Discussion

In this paper, we draw a distinction between intensity of effect—the percentage of taxa killed in a time interval (or the ecological effects of an extinction [Droser et al. 2000; McGhee et al. 2004])—and intensity of cause—the intrinsic physical intensity of the causal killing mechanism. So far, we have said little about the nature of the killing mechanisms; in fact, this catch-all term probably encompasses a wide range of processes. In some ''background extinction'' intervals, the so-called killing mechanism may consist of no more than low-intensity local processes uncorrelated among regions, whereas mass extinctions can result from a range of globally consequential phenomena (e.g., Alvarez et al. 1980; Sheehan 2001; Joachimski and Buggisch 2002; Bond et al. 2004; Erwin 2006). On the other hand, Peters (2005, 2006) offered support for sea level as at least a partial control on diversity fluctuations throughout much of metazoan history. Given such potential variation in the causes of extinction through time, is it appropriate to speak of ''intensity of cause'' in a simple, uniform manner?

Several lines of evidence suggest that our model is useful as a first-order analysis. Classes have similar susceptibility to extinction in times of background and mass extinction (Fig. 5), suggesting that variation in killing mechanism does not invalidate our approach. The match between the actual extinction history of individual classes and the model predictions (Fig. 6) also suggests that variation among intervals in the causes of extinction do not overwhelm the model. However, the logistic regression model assumes that the extinctions in each substage are not selective among classes in unique ways, which may not be true, especially for some of the mass extinctions (e.g., Sheehan and Fastovsky 1992; Knoll et al. 1996, 2007; Smith and Jeffery 1998). For example, Knoll et al. (1996, 2007) argued that the Permian/Triassic extinction was more severe for organisms vulnerable to hypercapnia (CO_2 poisoning). Extinctions that are uniquely selective for a subset of taxa may show up as instances of imperfect fit between our model predictions and observed data, but, as discussed, the model as a whole seems to fit well despite these effects.

In contrast with analyses such as those of Alroy et al. (2001), many of our analyses reinforce conventional views rather than overturning them. That being the case, the value of this paper may lie in (1) introducing a method by which extinction rates can be adjusted to account for taxonomic susceptibility, rather than interpreting such rates literally; (2) using the method to estimate the intensity of cause of Phanerozoic mass extinctions, as distinct from their intensity of effect; and (3) using the method to quantify effects that were previously known only qualitatively. As an example of the last point, we note that several authors have previously attributed the Phanerozoic decline in background extinction to the sorting of higher taxonomic groups (at various levels), with highly volatile groups being replaced by less volatile ones over time (Stanley 1979, 2007; Sepkoski 1984, 1991; Van Valen 1985, 1987; Gilinsky 1994). However, our study directly quantifies the extent to which this replacement of higher groups explains the decline in background extinction. Our analysis shows that changes in susceptibility at the class level are not sufficient to explain the decline in background extinction: only 29% of the decline can be attributed to such changes

in susceptibility. The rest must be due to changes in susceptibility at other taxonomic levels, or other factors such as changes in ecosystem structure, overall improvement in fitness, or expansion of geographic ranges (e.g., Jablonski 2005; Payne and Finnegan 2007). In fact, biological correlates of taxonomic affinity presumably underlie the differences in extinction susceptibility among classes noted in Table 4; however, taxonomic affinity is an efficient way of capturing significant variation in susceptibility.

We anticipate that our methodology may be extended to other situations, such as the dissection of class-level taxa (e.g., cephalopods) into finer components to elucidate their Phanerozoic-scale diversity dynamics, or the application of susceptibility to groupings not based on taxonomy (e.g., trophic level, life habit). Indeed, the statistical and biological issues that we have raised here apply to any study of rates of extinction (and origination as well) in which subgroups vary in rate and shift through time in proportion, including new studies using sampling-standardized data. If a higher proportion of taxa die in one interval than another, and we would like to know why, it may be incorrect to assume prima facie that the killing mechanism was intrinsically more severe. To avoid misleading conclusions stemming from statistical artifacts such as Simpson's paradox, we must account for the characteristics of the fauna extant in that interval.

Conclusions

1. The measured rate of extinction in an interval of time is affected by both the intensity of extinction triggers and the susceptibility of the fauna. Taxonomic classes are variably susceptible to extinction and constituted changing proportions of the global fauna through time, so the susceptibility of the global fauna to extinction varied through time.
2. Logistic regression can remove the effects of taxonomic susceptibility on observed extinction rates, yielding estimates of what extinction rates would have been if a fauna of constant composition existed through the Phanerozoic. Adjusted and observed

extinction rates are not entirely dissimilar, but several interesting patterns emerge from the analysis.
3. Taxonomic susceptibility declined through the Phanerozoic as susceptible classes were replaced in dominance by less susceptible classes. Thus, observed rates of extinction in the Paleozoic somewhat overstate the intensity of the causal ''killing mechanisms'' relative to later times.
4. Trigger mechanisms from early mass extinctions would have had lower rates of extinction on more recent, less susceptible faunas. Adjusting for susceptibility, the end-Permian extinction had the most intense cause, the Ordovician, Guadalupian, Triassic, and Cretaceous were all similar, and the Late Devonian had the least intense cause.
5. The susceptibility of taxonomic classes was largely similar in mass extinctions and ''background'' time intervals.
6. Mass extinctions did not occur in times of unusual susceptibility, although susceptibility sometimes increased in their aftermath (notably, in the Early Triassic).
7. The evenness of the taxonomic composition of the global fauna was inversely correlated with extinction rate in both the Paleozoic and the Mesozoic. In both cases, extinction was high and evenness was low early in the era (i.e., in the Cambrian and Triassic). Statistical evidence for a causal link between evenness and extinction rate is lacking, but ecological, environmental, and evolutionary similarities between these two periods may explain the similarity.

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