

# EXTINCTION VULNERABILITY AND SELECTIVITY: Combining Ecological and Paleontological Views

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## ABSTRACT

Extinction is rarely random across ecological and geological time scales. Traits that make some species more extinction-prone include individual traits, such as body size, and abundance. Substantial consistency appears across ecological and geological time scales in such traits. Evolutionary branching produces phylogenetic (as often measured by taxonomic) nesting of extinction-biasing traits at many scales. An example is the tendency, seen in both fossil and modern data, for higher taxa living in marine habitats to have generally lower species extinction rates. At lower taxonomic levels, recent bird and mammal extinctions are concentrated in certain genera and families. A fundamental result of such selectivity is that it can accelerate net loss of biodiversity compared to random loss of species among taxa. Replacement of vulnerable taxa by rapidly spreading taxa that thrive in human-altered environments will ultimately produce a spatially more homogenized biosphere with much lower net diversity.

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## INTRODUCTION

Extinction selectivity, or relative vulnerability, is of growing interest in both ecology (1, 3, 62, 93) and paleontology (49, 74, 75, 105). Despite the great difference in scale of observation in the two fields, much evidence about which groups are more likely to become extinct is consistent. Such evidence indicates a largely untapped potential for understanding why biased extinction is

common at many scales. For conservation biology, the importance of understanding extinction proneness is to “provide a basis for proactive conservation,” instead of current approaches that are largely “reactive and piecemeal” (1, p. 144). The increasing scale of biodiversity loss will require proactive measures that go beyond the population scales that have characterized most of conservation biology, to examine extinction risk differences among taxa and habitats (46, 71).

Applying fossil data to modern extinction problems is desirable because they document extinctions across large scales of time and space (48, 49). Also, such data provide our only opportunity to study “natural” extinction patterns. Human impacts have been so profound that not a single case of nonanthropogenic species extinction can be documented in the last 8000 years (16). Furthermore, nearly all of today’s anthropogenic causes of extinction, including habitat loss and biotic exchanges, were also major causes of extinctions in the geological past (48, 49).

I examine the best-studied biological traits that influence risk, especially those defining “generalist” taxa. I then examine ecological and fossil evidence on how these traits are nonrandomly distributed among three basic categories of biodiversity: 1. populations and species, 2. higher taxa, and 3. geographic biotas. This nonrandomness identifies three major areas of risk assessment that need urgent scrutiny by conservation planners. For example, evolution has nonrandomly nested species risk among higher taxa (62, 74).

## BRIEF HISTORY OF THOUGHT ON EXTINCTION VULNERABILITY

That some groups are at greater risk of extinction is an old idea. Lamarck speculated that marine organisms were less prone to extinction than terrestrial organisms because they were more “buffered” against environmental change (15). In *Principles of Geology*, Charles Lyell (63) devoted two chapters to a surprisingly modern discussion of the selective nature of extinction. Examples include extinction of cold-intolerant plants during times of climatic cooling and the higher risk of extinction in species with narrow geographic ranges. Darwin devoted considerable attention to dominant species that resisted extinction because they were both more abundant locally and had a very wide geographic range (10). Another early theme still common in modern discussions of species risk (e.g. 78, 80) is that of generalist species. Simpson (96), for example, argued that broadly adapted species persisted longer in the geological record.

The dawning “extinction crisis” in the 1960s led to a flurry of ecological studies in the 1970s that produced a rapid growth of publications, especially in ecology, about extinction proneness. Ehrenfeld (21) produced an influential

list of factors promoting species extinction risk that is still used in textbooks (45, 78, 80): specialized habitat preferences, restricted distribution, intolerance of human presence, reproduction in aggregates, low fecundity (low litter size, slow maturation, long gestation), large size and predatory habits, less adaptable behavior patterns, and excessive hunting. Another commonly cited list is Terborgh's (102): high trophic level, largest guild members, poor dispersal ability, continental endemics, island endemics, colonial nesting, and migratory habits. Terborgh's list (and many others) reflects the influence of bird studies, where many risk data continue to originate (54, 55, 56, 65). Current articles and books discussing traits extinction risk in both ecology (45, 78, 80) and paleontology (48, 88, 89) typically draw heavily, if not entirely, on these early lists.

### *Nonrandom Extinctions in Ecological and Geological Time*

Brown (10) discussed the traditionally dichotomous approach that ecologists have taken toward extinction, regarding it as either deterministic or stochastic. A similar dichotomy has existed in paleontology, illustrated in Raup's (88) subtitle *Bad Genes or Bad Luck*. Hedrick and others (41) argued that this dichotomy is artificial and largely reflects our ignorance of the complex processes that create stochastic patterns.

My present concern is with the role of this dichotomous view in discussions of selectivity, or relative risk between groups. One of the most general deterministic ecological patterns is the similar composition of depauperate subsets found in modern faunas that represent fragments of formerly more species-rich faunas. Global warming since the last glacial episode has isolated once-continuous bird and mammal faunas on mountain ranges and on islands due to sea level rise. A number of studies (e.g. 10, 19) show that "extinction is a highly deterministic process: extinctions occurred in approximately the same sequence throughout the region, despite wide variation in extinction rates" (19, p. 496). The sequence of extinction can often be related to specific traits. Species with large body size, high trophic level, specialized habitat needs, and poor dispersal are among the most consistently extinction-prone, and they disappear from all but the largest "islands" (10, 19). These same nested patterns are also found in studies of current habitat fragmentation of modern ecosystems. Mammals (60), birds (20, 56, 102), and plants (103), for example, show that the depauperate subsets of the smallest remnant habitats tend to consist mainly of small, generalized, and widely dispersing species.

Nonrandom extinction is also very common in the fossil record. Despite persistent claims of evolutionary randomness (34), both background and mass extinctions consistently show nonrandom ecological and taxonomic patterns

of extinction, discussed in detail below. A key observation by Jablonski (49, p. 34) is that modern extinctions so far “conform mainly to intensified versions of background expectations.”

## TRAITS PROMOTING EXTINCTION VULNERABILITY

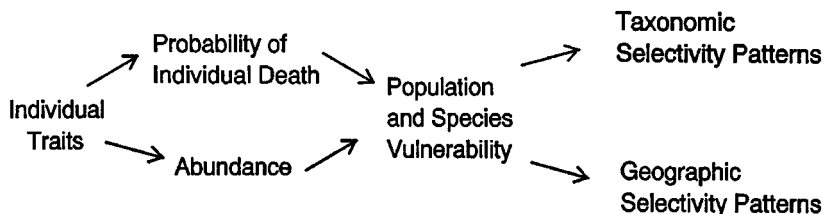
Population extinction can be fruitfully viewed as “correlated death” of individuals (39). When population size is large enough to avoid the intrinsic extinction causes of genetic and demographic fluctuations, it generally takes one or more extrinsic environmental perturbations to cause such correlated death of a population and species (59). These perturbations can be categorized in a variety of ways such as Diamond’s (20) “evil quartet” of habitat loss, species introductions, extinction cascades, or overexploitation, and they can occur over many time scales.

Figure 1 illustrates how the traits cited as promoting population extinction risk, often in both ecology and paleontology, can be separated into categories that influence the risk of population extinction via “correlated death” by external perturbations.

### *Individual Traits*

The most basic category consists of traits of the individual organism. Most extinction-biasing traits discussed in both ecology and paleontology are in this category. Examples listed in Table 1 include specialization and large body size.

Individual traits can increase population extinction risk by their effect on (a) probability of death per individual, and (b) number of individuals. For example, other things being equal, the risk of correlated death generally increases as probability of individual death increases and mean abundance decreases. Other things are rarely equal, and the interaction among these variables can be complex, as demonstrated by life history theory (101) and population biology



*Figure 1* Individual traits influence extinction by their effect on the probability of individual death and on abundance. This translates into population and then species vulnerability. Phylogenetic nesting of species vulnerability among taxa from evolutionary constraints results in nonrandom taxonomic and geographic patterns of selectivity.

**Table 1** Biological traits cited in the ecological and paleontological literature as increasing extinction risk. Symbols: ++ = many citations identified, + = at least one citation identified, - = none identified so far. Citations for modern extinctions are 5, 10, 20, 21, 29, 30, 45, 61, 62, 78, 80, 84, 92, 102, 108. Citations for fossil extinctions are 2, 8, 22, 29, 48, 49, 51, 66, 72, 75, 86, 89, 95, 99, 100, 105

	Modern extinctions	Fossil extinctions
<u>Individual Traits</u>		
Specialization:	++	++
* Stenothermy	++	++
* Specialized diet	++	++
* High trophic level	++	++
* Symbiotic	++	+
* Large body size	++	++
* Low fecundity	++	+
* Long-lived	++	+
* Slow growth/development	++	+
* Complex morphology	+	++
* Complex behavior	+	+
* Limited mobility	++	-
* Migratory	++	-
Aquatic biotas:		
* Planktic	+	++
* Epifaunal	+	++
* Filter-feeder	+	++
- Coarse-filter feeder	-	+
* Non-benthic larvae	+	+
* Non-brooding larvae	-	+
<u>Abundance Traits</u>		
Low mean abundance (K):	++	++
* localized range	++	++
* low density	++	++
High abundance variation	++	+
Low intrinsic growth (r)	++	-
Seasonal aggregations	++	-
Low genetic variation	++	-
Aquatic biotas:		
* Small colonies (corals)	-	+

(84). However, Figure 1 does help differentiate between two major categories of risk traits that are usually lumped together: traits that describe the individual versus traits that describe the population.

Table 1 summarizes the individual traits most commonly found in the ecological and/or paleontological literature. It is far from exhaustive and should be viewed as an initial attempt to compare the relative frequency with which various traits are cited in the literature. General sources for this Table include many excellent reviews (and citations within them) of extinction-biasing traits cited in the caption. Additional references are discussed below.

Table 1 shows that, despite the immense differences in temporal and spatial scales of observation between ecological and geological data, there are many consistencies. Some cases in which these scales do not agree seem to stem from scale differences in sampling. Ecological data on extinction risk are much better for terrestrial than marine biota (71), whereas the reverse is true for the fossil record (49). Because space does not permit a detailed discussion of Table 1, I focus on two major themes that subsume many key practical and theoretical issues—specialization and body size.

### *Specialization*

Many traits in Table 1 are associated with the idea that extinction-prone organisms are “specialized” or narrowly adapted. In fact, specialization is arguably the most fundamental concept in the history of thought on extinction risk. More than 20 years ago, Wilson & Willis (108) referred to “truncation of ecological guilds” as the “well-known but seldom emphasized early loss of specialists and large species.” Since then, evidence for this has continued to accumulate, and specialization is found in virtually all conservation textbooks as a major trait promoting extinction (e.g. 45, 78, 80). Similarly, many paleontologists have emphasized the extinction resistance of generalist species in both background and many mass extinctions (8, 72, 75, 99, 105).

Many extinction-promoting traits are associated with being specialized (Table 1). This implies that such traits may covary. Covariation is supported by the growing evidence for Brown’s “niche-breadth hypothesis” (10) that niche breadth tends to covary among niche parameters, so that a species broadly adapted in one parameter such as temperature tolerance is also broadly adapted in other parameters such as diet (10, 28, 61, 62). There is also evidence that niche narrowness is related to decreased local abundance and decreased geographic range (10, 61, 62). Specialized species may thus be prone to multiple jeopardies produced by a synergistic combination of fewer individuals with narrower tolerances to change (61, 62). Among living freshwater fish, for example, specialization is correlated with extinction-proneness by limiting geographic range and also by increasing sensitivity to anthropogenic environmental changes

(1). At paleontological scales, this may explain why tropical taxa tend to have higher evolutionary turnover rates (see below).

Explanations of extinction risk in terms of specialization have been plagued by poorly defined terms (28). Not specifying the valid taxonomic and phylogenetic scales of comparison has often confused the issue. A classic illustration is the traditional *r-K* paradigm, which is widely recognized as invalid at the population level for which it was originally formulated (73, 101). But Stearns (101) noted that many of the original assertions of the model are true at higher taxonomic scales of comparison because clade-level life-history and related traits tend to become embedded relatively early in development. They are thus shared by all species in the clade. Mammals, for example, are more specialized and *K*-selected than insects, in terms of being longer-lived, larger, and less abundant (14), and having other classic *K*-selected traits (many of which are listed in Table 1). This is also true of coarse comparisons within the mammals, where rodents are more generalized and *r*-selected than large mammals (14). Such generalizations may contribute to our understanding of why some clades (however defined) are more at risk than others.

At finer taxonomic and phylogenetic scales of comparison, we thus might not expect broad generalizations of strict covariance among traits to hold as often as generalizations made among coarse scales (101). For example, a phylogenetic analysis (6) showed that, among British birds, species with fast development tend to be abundant, as predicted by *r-K*. But no life history variables consistently correlated with abundance within taxa (6). Estimates of relative extinction risk should thus specify exactly the taxonomic and phylogenetic levels and the traits. The increasing use of phylogenetic analysis and the comparative method among ecologists (40) promises to do this and may greatly increase the precision of extinction-risk estimates. An excellent example is Gittleman's (31) phylogenetic analysis of the giant panda. He showed how its high extinction risk arises from having an exceptionally slow development, low fecundity, and other high-risk traits compared to related species.

The large majority of risk traits in Table 1 were deduced from data that did not include detailed phylogenetic information. Rather, the data were based on comparisons of extinction rates among related taxa. For example, extinction selectivity within bird guilds is among the best-studied patterns. Studies of tropical forest fragmentation showed that large frugivores and large insectivores are the first groups to go extinct in small fragments (56). Such ecological patterns of selectivity translate into taxonomic patterns because the species most at risk are not randomly distributed among the families studied (see below). Extinction patterns among related taxa after habitat fragmentation are also well documented in mammals (60) and plants (103): Poorly dispersing species of mammals and plants tend to go extinct sooner than widely dispersing

relatives. In addition, a few generalized species tend to increase in abundance (108).

Paleontological patterns of selectivity against specialists in Table 1 have usually been, not surprisingly, derived from analyses of coarse taxonomic patterns. However, comparisons of species-level with genus- and higher-level selectivity patterns generally yield the same patterns (4, 27). Foote (26) reviewed evidence that fossil taxonomic patterns are generally valid indicators of underlying phylogenetic patterns.

### *Body Size*

Large body size is one of the most commonly cited traits promoting extinction in both ecology (10, 45, 78, 80) and paleontology (48, 73, 105). In some cases, large body size has itself been seen as a type of specialization (97). In other cases, large size has been viewed as a correlate of specialization, as in the traditional *r-K* paradigm (14, 73, 101). In still other cases, the most extinction-prone species are described as the largest and most specialized of a feeding guild (55, 56, 102), indicating that large size and specialization can be independent traits.

Even when large body size is separated from other risk-promoting traits, it is not a universal predictor of extinction. Studies can be found reporting positive, negative, and no relationship between body size and probability of extinction (5). A main reason for these discrepancies is that these studies “concern a variety of taxa, in different habitats, at different spatial scales and whose extinction has been caused by different processes, and so are difficult to reconcile” (5, p. 472). These scaling differences produce different results because body size influences population abundance (29, 30, 62) and fluctuations (29, 30, 62, 84) in complex ways that differ among taxa.

We may therefore expect to find that body effects on extinction will vary among taxa. In the aquatic realm, in marine invertebrates and freshwater fish, large size apparently does not increase extinction risk. Jablonski (50) found that, at least for mollusks in the late Cretaceous (K-T) mass extinction, body size was not a factor in determining species survivorship. He suggested that this was because dispersal ability and geographic range—factors known to strongly influence molluscan extinction resistance (49)—are not correlated with body size. Similarly, small body size often promotes extinction in freshwater fish, perhaps because small fish disperse poorly (1).

In contrast, large body size in terrestrial vertebrates is often correlated with increased geographic range and many other traits that affect extinction probability (10, 11, 14, 73). In particular, two general patterns seem to emerge. One is based on the finding that, of closely related species, the larger is often more abundant, perhaps because of competitive advantages (18). We might



thus predict that populations of large-bodied species are less extinction-prone than populations of closely related smaller species. Data are scarce, but this is apparently true in shrews (83) and some birds (33).

A second prediction is that, of more distantly related taxa, large body size increases extinction proneness because of the commonly discussed liabilities of large size in the “mouse-to-elephant” curves (14, 73). Much evidence, from both fossil and modern extinctions, seems to support this. In Brown & Nicoletto’s study (11), 11 of 13 mammal species that disappeared from 24 local habitats in North America weighed more than 2 kg. Among birds, both globally endangered species and historically extinct species (since 1600) tend to be larger than average (5).

Similar patterns are seen at the coarse taxonomic scales of comparison in fossil vertebrate extinctions. In his overview of the K-T extinctions, Archibald (2) reported that 57% of large (over 10 kg) vertebrates went locally extinct at the Hell Creek site compared to 30% of small vertebrates. Large mammal species had lower survivorship than smaller species during the late Pleistocene megafaunal extinctions (66) and apparently during most background time (98). However, in the late Eocene extinctions, large-bodied mammal species were not selected against (106). This points out the importance of external causal mechanisms; the late Eocene extinctions were generally related to global cooling (86), and large body size is often favored in endotherms (14, 73).

### *Abundance Traits*

Abundance can be seen as a derived trait of more basic individual traits (Figure 1). Abundance at any time is produced by the interaction of intrinsic individual traits, which determine individual survival and reproduction, with the extrinsic abiotic and biotic environment. Rarity is often cited as the single best predictor of extinction likelihood across many scales (29, 65, 100). Abundance is also easier to measure than many individual traits, such as mean body size, complexity, mobility, and developmental rate.

Gaston (29) discussed the many ways that rarity, or low mean abundance, can be described. Two of the most common ways are included in Table 1: localized geographic range and low density. Both of these metrics are strongly correlated with increased extinction rate on ecological (29, 84, 92) and geological (48, 49, 75) scales. There are many exceptions, however. A substantial number of abundant, widespread species have become extinct through human activity (92, 107).

The influence of rarity on extinction depends on taxonomic scale and the types of rarity examined. According to an exemplary study by Mace & Kershaw (65), for South African birds, small population size is a better predictor of extinction risk than small geographic range or habitat specificity. A neglected type of rarity

is artificial rarity, i.e. formerly abundant species now decimated by humans. Species displaying this type of rarity may be much more likely to go extinct than species that are evolutionarily adapted to rarity (58).

The two types of rarity in Table 1 are not independent. There is evidence at many scales that geographic range and local abundance are generally correlated so that widespread species tend also to be locally dense (10, 29, 36, 61, 62). Brown's niche-breadth hypothesis is that this correlation occurs because broadly adapted species are able to exploit a wide range of resources, both locally and geographically (10). However, other factors are also likely involved in this correlation. Metapopulation dynamics, for instance, indicates that locally rare species are more likely to have a narrower geographic range because they have poorer dispersal and thus fewer source populations (36). A major implication of both the niche-breadth and metapopulation explanations is that rare species are faced with synergistic forces that may make them much more prone to extinction than abundant species (61, 62). In addition to being more localized, sparse, and relatively more specialized, rare species have more fragmented geographic ranges that can amplify population decline through metapopulation and edge effects (70).

Two other important abundance traits in Table 1 are high abundance variation and low rate of intrinsic growth. Other things being equal, a population with greater temporal variation will have a greater probability of extinction than one with less (84). But other things, such as spatial distribution, life history, and other variables, are rarely equal (61, 62). This is apparently why a consistent relationship between temporal abundance variation and extinction probability was not found in the extensive survey by Gaston & McArdle (30). The role of spatial distribution is especially evident given the recent findings that variation in spatial and temporal abundance are correlated. Species with patchy, highly variable spatial abundance also tend to have highly variable temporal abundance (10, 69). Fossil foraminifera species with higher spatial abundance variation also tend to have higher temporal abundance fluctuations (77).

Low intrinsic growth rates can contribute to extinction by reducing what Pimm (84) has called "resilience," i.e. the ability of a population to rapidly recover from disturbances. Empirical evidence is seen in Amazonian mammals; hunting has caused higher local extinction rates among primates than in artiodactyls and large rodents because of primates' lower intrinsic growth rates (7).

### *Population Vulnerability Versus Species Vulnerability*

Conservation texts often imply that population vulnerability and species vulnerability are correlated (45, 78, 80). Even a current overview on population dynamics of extinctions has "not made a distinction between the local extinction

of populations, and the global extinction of species" (62, p. 148). On the other hand, Brown (10, p. 164) warned that "it is hazardous to make sweeping predictions about species extinctions and conservation policy from studies of small populations. . . ." For example, one of the primary messages of metapopulation dynamics is that species with high population turnover (extinction and recolonization) can, in theory at least, have relatively low species turnover (36–38, 77).

Three emerging lines of evidence tentatively imply that population risk is generally correlated with species risk. More cautiously, this evidence indicates that species risk is not independent of population risk.

The first line of evidence is the documentation by Harrison (37, 38) that many, perhaps most, species do not have classic metapopulation structures, consisting of population patches in an equilibrium state of local extinction and recolonization. Instead, species persistence often depends on one or a few large mainland or "source" populations that track or migrate along with environmental changes. The vulnerability of these source populations would likely be good indicators of species vulnerability. Alternatively, some mobile species maintain a very patchy population structure, with substantial gene flow within the species range, so it is essentially a single large population. Again, the vulnerability of this population to environmental change would seem to be a good indicator of species risk.

The second line of evidence is the nested, predictable sequence of population extinction discussed above, in which the same species tend to be the first to go locally extinct (10, 19). This sequence indicates that population vulnerability will ultimately translate into species extinction as losses accumulate. Thus, bird species that disappeared earliest on Barro Colorado Island also tended to have lower survival rates on the mainland (54). Similarly, species that are most at risk globally are often the first to disappear from local communities. For example, primate species are among the most imperiled mammals globally (46), and they are also among the first mammal species to disappear locally (7).

The third line of evidence is that the same traits that population extinction risk, such as specialization and rarity, also seem to explain increased extinction rates among species and higher taxa. Low intrinsic rate of population increase, long generation time, and long lifespans have been used to explain high rates of extinction (or threat) in primate populations (46) and in primate species (7).

## EXTINCTION VULNERABILITY AMONG TAXA

Phylogenetic constraints can nonrandomly affect population and species extinction vulnerability (risk) in many ways among taxa because body size,

abundance, niche-breadth, and many other extinction-biasing traits in Table 1 have a significant genetic (heritable) component (29, 61, 62). Evolutionary branching can therefore concentrate extinction-biasing traits into certain taxa at many taxonomic levels. Specific evidence for this includes the nonrandom taxonomic clustering of rare species in some North American bird families (68) and plant families (94), widespread species in some genera of living echinoids (74) and fossil mollusks (47), and large-bodied birds in some higher taxa (5, 6). The rise of the comparative method, especially as applied to ecological traits (40), should soon provide many crucial insights into such patterns.

Understanding phylogenetic effects on extinction vulnerability is crucial to maximizing biodiversity because, as Foote (24, 25) has shown in many fossil taxa, highly selective extinction can reduce biodiversity much more than random extinction. When species extinction is highly concentrated within certain higher taxa (or areas of morphospace), there is a greater loss of net diversity than when similar amounts of extinction are randomly distributed among species. This has troubling implications for today's extinction crisis which, as discussed next, shows considerable evidence for nonrandom extinction at many taxonomic levels.

### *Vulnerability Differences Among Higher Taxa*

A large literature documents consistent taxonomic differences in fossil (49, 51, 75, 91, 100, 105) and modern (46, 71) species extinction rates among very high taxa such as classes or orders. Fossils indicate that these extinction patterns are often consistent both across "background" geologic time and during mass extinctions (22, 49, 51, 72, 91, 100, 105), indicating that the same groups are generally less susceptible to extinction from all possible causes.

Table 2 summarizes some of the recent data on average extinction rates in fossil taxa, expressed in terms of average species duration. There are many uncertainties in these estimates, and they are only averages of a wide range of species durations in each taxon (49). But the estimates for each taxon have been surprisingly stable since Simpson began his early estimates in the 1940s (98). Also, modeling results indicate that extinction rate differences, such as lower rates for bivalves than mammals, cannot be attributed solely to differences in fossil preservation potential (27). Finally, there is tentative agreement with modern extinction rates. Fossil primates, for example, have a relatively shorter species duration than other mammals (Table 2), in agreement with modern data that primates are more extinction-prone from human activities than are most other mammals (7, 46).

A key implication of Table 2 is that marine taxa are consistently less vulnerable than terrestrial taxa. This can be viewed statistically: The probability that all six land taxa (counting the three mammal entries as only one) would end up

**Table 2** Estimated mean duration of fossil species. Except insects, invertebrate data are for marine species. Where estimates involved a range of values, the midrange value is shown

Taxon	Species duration	
	(my)	Reference
Reef corals	25	100
Bivalves	23	100
Benthic forams	21	12,13
Bryozoa	12	43
Gastropods	10	100
Planktic forams	10	81
Echinoids	7	100
Crinoids	6.7	4
Non-marine		
Monocot plants	4	100
Horses	4	44
Dicot plants	3	100
Freshwater fish	3	100
Birds	2.5	100
Mammals	1.7	100
Primates	1	67
Insects	1.5	100

as the six highest out of 14 total entries due to random independent sorting is about 1% (76).

Are the inferences drawn from fossil data valid for modern human-caused extinction dynamics? Figure 2 plots the fossil species duration data from Table 2 against the percentage of threatened species within each taxon using a recent compilation (71). There is a fairly high correlation between the modern and fossil data. As with the fossil extinction data, worrisome biases appear in the estimates of threatened living species. In particular, both fossil (49, 89, 90) and modern (71) extinction data tend to underestimate the number of extinct or threatened species because many rare species are often not recorded. Given these caveats, the pattern in Figure 2 is that terrestrial taxa tend to be more vulnerable to extinction today, as in the past (76). This provides tentative quantitative support to the conventional wisdom that marine species are less prone to extinction (15, 82). Direct evidence indicates only four confirmed modern extinctions of marine invertebrates, all gastropods (15).

As Jablonski (51) noted, it is difficult to relate the differences in vulnerability among such higher taxa to specific biological variables. We can, however, point

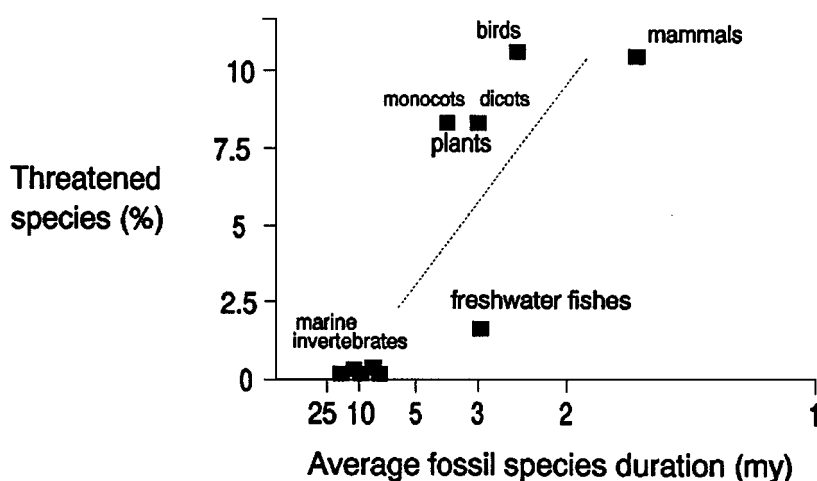


Figure 2 Proportion of species in a group that is currently threatened versus average fossil duration of species in that group. Regression line is least squares.

to direct fossil evidence that persistence of higher taxa is strongly influenced by two variables, the number of species and the resistance of each species to extinction. Increased species-richness has been documented to increase the geological persistence of many higher taxa (48,49). Such taxa may be at considerable risk during the modern extinction crisis if they rely on high rates of speciation to replace frequently lost species, should anthropogenic reduction of speciation occur.

The other factor, differences in species extinction resistance, is important because without it, very diverse clades would never die out (89). Such differences are apparent in Figure 2, in which some higher taxa, especially marine, seem to have reduced species vulnerability. In this case, a broad biological explanation for the pattern is the common suggestion that marine species tend to have wider geographic ranges than do terrestrial species (82). Rapoport (87) quantified this in a comparison of geographic ranges between marine and terrestrial species. He derived an index of cosmopolitanism four times higher in marine than terrestrial species. This is consistent with findings that geographic range is a primary determinant of fossil species persistence in marine taxa (49,50).

### *Vulnerability Among Lower Taxa*

Comprehensive comparisons of species extinction rates among lower taxa such as families are often difficult. Major reasons for this include the difficulty of

accurately estimating fossil and modern species extinction rates, noted above, and of accurately reconstructing phylogenetic relationships (26, 32, 40). Fossil studies suffer the additional burden that many of the traits influencing extinction-proneness (see Table 1), such as physiological and life-history parameters, are not preserved. This obstructs efforts to explain patterns of differential extinction. For example, McKinney (74) found evidence that extinction has been concentrated in certain genera of echinoids over about the last 75 my. But, aside from the fact that widespread species are clustered within certain modern echinoid genera, it was impossible to determine what caused the nonrandom fossil extinctions. More information on vulnerability among lower taxa is obviously available for living species. Phylogenetic analysis shows that carnivores tend to have higher extinction rates than most other mammals through geologic time (32).

The most useful data on taxonomic vulnerability patterns come from studies of historical anthropogenic extinctions. The findings of Kattan et al (56) show that forest fragmentation strongly impacts large frugivorous and insectivorous birds and disproportionately affects such major taxa as parrots, toucans, and antbirds (55). Kattan (55) cited other studies showing that bird families such as Columbidae were more resistant to Pleistocene extinctions than other families such as Picidae and Cracidae because of phylogenetic nesting of dietary, body-size, and abundance traits. An example among plants is that the cactus family, Cactaceae, contains a disproportionately high number of extinct and endangered species, because of the generally restricted habitat and specialized adaptations of the family (42).

A predictive approach to future vulnerability patterns has been pioneered by Russell and others (93) in a study of recent bird and mammal extinctions. Data on the extinction rate of these two groups are of the highest quality of all major groups because of popular interest in them (46). Using rarefaction techniques, Russell and others (93) found that bird and mammal species' extinctions since 1600 are nonrandomly concentrated within species-poor genera. Much of this selectivity in birds was due to the high extinction rates of endemic island birds (e.g. rails), which are often evolutionarily isolated and tend to be classified into their own genera (93). The causes in mammals seem to be more complex, with multiple types of ecological selectivity including overhunting and effects of large body size.

Russell and others (93) predicted future selectivity by applying a probability formula from Mace (64) to species now listed as threatened on the IUCN Red List (46). Future bird extinctions are predicted to have less taxonomic selectivity than in the past (93). This projected decrease in selectivity may occur because island bird faunas have already been so devastated that future extinctions will largely concentrate on continental bird populations containing

more species-rich faunas (93). Mammals may show declining future selectivity (93) because widespread habitat loss on continents is replacing more selective extinction causes such as overhunting of large mammals (46).

## EXTINCTION VULNERABILITY AMONG GEOGRAPHIC BIOTAS

The extinction vulnerability literature contains three major categories of habitats that are often contrasted: terrestrial-marine, island-continental, and tropical-nontropical, where the first of each pair is usually considered to contain more extinction-prone species. Such habitat, or geographic, categories are seldom independent of taxonomic extinction patterns. Evolutionary diversification within regions produces phylogenetic proximity that is often correlated with geographic proximity (9).

The terrestrial-marine pair illustrates a relationship between taxonomic and habitat vulnerability. Higher taxa in the marine environment tend to have lower extinction rates than mainly terrestrial taxa (Figure 2). This appears true for both the current extinction crisis and past geological background extinctions (76). In addition to having more widespread species, the marine environment may buffer species from rapid physical changes (82). Within the marine realm, deep-water species seem to have preferentially survived the late Devonian (72) and late Permian (22) mass extinctions. Similarly, the current extinction crisis is most strongly affecting shallow, nearshore habitats (82).

One terrestrial habitat—freshwater—deserves special mention. The very high modern extinction rates in these systems seem to be matched by relatively high turnover rates during geological time (Figure 2). However, some mass extinctions apparently showed the opposite effect—preferential survival of freshwater biota compared to marine biota. The global cooling that caused the late Devonian extinction (72), and the sea level fluctuations and meteorite impact that caused the late Mesozoic extinction (2) are both characterized by nonrandom survival of freshwater biota. This has been attributed to the ability of freshwater biota in the late Devonian to better tolerate seasonal and other physical fluctuations (72). Freshwater biotic survival of the late Cretaceous meteorite impact has been related to a detritus-based food web that buffered the effects (95). The high extinction rate of freshwater species today (46, 78, 80) is apparently because the causes are so multifaceted, including pollution, dams, exotic species, and other disturbances (78, 80), that any advantages in tolerance or buffering effects relative to marine habitats are overwhelmed.

For modern extinctions, island species are well known to have generally higher rates than continental species (45, 46, 78, 80, 84). Thus, the fossil record



notably shows that islands have often provided refugia during mass extinctions, particularly for marine taxa; many higher taxa may have survived on such refugia during times of sea level lowering (52). In recent times islands near New Zealand have served as refugia to transplant ground birds threatened by European exotics (45).

Higher extinction rates of tropical species compared to nontropical species are well documented for modern times (46, 62, 71, 78). This disparity also seems to occur at geological time scales. Briggs (8) and especially Flessa & Jablonski (23) reviewed the considerable evidence from marine groups that tropical species are geologically younger and, on average, have higher extinction rates than nontropical species. This could be due to narrower ecological tolerances and/or narrower geographic ranges of tropical species (8, 23). In past mass extinctions, including the late Devonian (72), late Permian (22), late Cretaceous (2), and some smaller Cenozoic extinction events (86, 99), tropical taxa have been preferentially eliminated. As today, tropical reefs have been consistently decimated during such mass extinctions (57).

## EXTINCTION FILTERS: PAST SELECTIVITY AND TODAY'S EXTINCTIONS

Ecologists increasingly appreciate that extinction patterns during the Cenozoic Era, especially since the Oligocene Epoch, may explain poorly understood vulnerability differences among living biotas (3, 17, 53). Two general areas are briefly reviewed here.

### *Climatic Filters*

Since the late Eocene, about 40 Mya, the earth's climate has undergone cycles of cooling. While these have caused no global mass extinctions, they have caused many regional extinctions on land and in the sea (86). Stanley (99) and Briggs (8) reviewed evidence that these cycles consistently produced impoverished, broadly adapted biotas by selectively eliminating tropical biotas. The warming cycle that followed these extinctions is characterized by the evolutionary rediversification of more specialized tropical forms that were affected during the subsequent cooling episodes.

That we are currently in an impoverished phase in the oceans is seen in the evidence that the severe cooling and sea level changes of the Pleistocene had little impact on marine biota, at least in the northern hemisphere (49, 53). Coope's review (17) made a similar point about land faunas, showing that ice-age insect faunas of western Europe experienced very little extinction. A basic theme is that these filtered, broadly adapted marine and terrestrial biotas are able to migrate, with shifting geographic ranges, in response to climate change

(17, 104). The implication for impending anthropogenic global warming is that these biotas may respond in the same way.

### *Human Filters*

Extinctions caused by humans before the modern extinction crisis are particularly important filters of current vulnerability. Perhaps the best known example is the role of humans in the geologically recent megafaunal extinctions of the late Pleistocene Epoch (66). Another example is the devastation of island bird faunas by human settlements (85). Previous loss of species that are most sensitive to human activities can, in an ironic way, be viewed as a positive sign in that the remaining species are likely to be less vulnerable (3). Some Pacific islands have experienced bird loss for thousands of years; the islands with the longest periods of human habitation have generally witnessed the fewest recent recorded bird extinctions (85). Such cryptic (unrecorded) extinctions seem also to have occurred in Mediterranean plants. Recorded historic extinction rates are much higher for plants in Australia and California than in the Mediterranean area, where intensive human settlement has existed for much longer (35).

A main implication of past filtering is that current conservation efforts should place greater emphasis on preserving areas where humans have had less impact. As Balmford (3) noted, this is where the greatest amount of relative biodiversity can be saved, especially in terms of effort expended.

## SYNTHESIS: BIOTIC HOMOGENIZATION AND THE SPREAD OF WEEDY TAXA

Traits that make populations more prone to extinction include: 1. individual traits, especially those related to narrow niches, and 2. abundance traits, such as low mean abundance and abundance fluctuations. The apparent lack of pure metapopulation dynamics in most species, along with other evidence, implies that these traits promote species extinction as well as population extinction. Evidence for Brown's niche-breadth hypothesis suggests that some species are extremely vulnerable because they have synergistic combinations of extinction-promoting traits. These include specialization and rarity with fragmented ranges. Such generalizations about extinction vulnerability are most useful in specific phylogenetic, or at least taxonomic, contexts. Large body size, for example, seems to increase extinction vulnerability in mammals, but not in many taxa of marine invertebrates.

A phylogenetic view also demonstrates that traits promoting extinction are not randomly distributed among taxa at many scales. This has enormous, largely unexplored, implications for conservation biology. Among very high taxa, marine organisms seem to be much less extinction-prone both now and in the geologic past. Selectivity among lower taxa is illustrated by the biased loss of

certain families of forest birds and by historical extinctions concentrated in certain genera and families of birds and mammals. Such selectivity may decrease as more widespread, catastrophic causes of extinction increase. Phylogenetic selectivity often translates into geographic selectivity as illustrated by terrestrial and tropical species, which are generally more prone to extinction now and have been in the past than are marine and nontropical species. Predicting future phylogenetic extinction selectivity allows biologists to detect patterns of vulnerability at many taxonomic scales while simultaneously considering the phylogenetic uniqueness of those taxa in making conservation decisions.

A crucial prediction of the vulnerability patterns reviewed here is that the future biosphere will clearly become progressively less diverse as the more extinction-prone taxa and subtaxa become extinct. This biodiversity loss will be increasingly magnified to the degree that phylogenetic and taxonomic selectivity are concentrated in certain groups; such selectivity produces disproportionate reduction of overall biodiversity (24, 25).

The converse of the patterns considered here is that of positive human selective impacts on some biota. Some taxa, generally categorized as commensals or weeds, not only have preferentially survived in human-altered environments but have thrived (79). The rapid spread of such taxa, in conjunction with the increasing extinction of more vulnerable taxa, will produce a biosphere that is not only less generally diverse, but also more spatially homogenized (10, 92).

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