

# Extinction

Andy Purvis,<sup>1\*</sup> Kate E. Jones,<sup>1</sup> and Georgina M. Mace<sup>2</sup>

## Summary

In the life of any species, extinction is the final evolutionary process. It is a common one at present, as the world is entering a major extinction crisis. The pattern of extinction and threat is very non-random, with some taxa being more vulnerable than others. **Explaining why some taxa are affected and some escape is a major goal of conservation biology.** More ambitiously, a **predictive model** could, in principle, be built by integrating comparable studies of past and present extinctions. We review progress towards both **explanatory and predictive frameworks**, comparing correlates of extinction in different groups at different times. Progress towards explanatory models for the current crisis is promising, at least in some well-studied taxa, but the development of a truly predictive model is hampered by the formidable difficulties of integrating studies of present and past extinctions. *BioEssays* 22:1123–1133, 2000.

© 2000 John Wiley & Sons, Inc.

## Introduction

The world is entering a major extinction spasm. Present rates of species extinction are reckoned to be between 1000 and 10,000 times the rates seen through most of geological history.<sup>(1–3)</sup> Understanding the patterns of extinction and threat is a major goal of conservation biology. It is important for two reasons. (1) Development of a powerful explanatory framework will identify those attributes that predispose species to go extinct or to survive in the face of human disturbance. (2) More ambitiously, a predictive framework would help us to predict outcomes of possible different future scenarios, helping us to minimise human impact on biodiversity.

What form would such frameworks take? Many studies (see later) have found variables that statistically predict extinction or extinction-proneness in a group of species in one place or habitat type. **Extinction probability is a function of (1) the particular characteristics of the organism and its phylogenetic group (clade), (2) a particular set of causal processes that affect survival and/or reproductive rates and (3)**

**the time scale during which these processes operate** (Fig. 1).

To take just one example, primate species in which individuals range widely show a greater decline than more restricted species when forests are degraded by selective logging.<sup>(4)</sup> Such studies, important in their own right, are the first pieces in a much larger multidimensional jigsaw. Which variables matter most, however, might depend upon what is causing the threat. If hunting, rather than logging, is the problem, then the species at greatest risk might be those with large individuals, slower reproductive rates and that are active by day.<sup>(5)</sup> The important variables may also differ among taxonomic groups showing very different adaptations: reproductive rate predicts vulnerability in carnivores but not in primates, for example.<sup>(6)</sup> Time is a third crucial dimension to the jigsaw. Nearly all the species that have ever existed are extinct. Analyses of the fossil record can both identify the process responsible for extinctions and implicate particular traits as shortening the odds for species displaying them.

Figure 1 shows these three dimensions of the jigsaw (others, like **geographic location**, are possible too). Each piece of the puzzle corresponds to a study of which attributes predisposed species of a group, living at a particular time, to go extinct in response to a particular kind of threat. If the individual studies can explain a high proportion of the variation in extinction risk or rate among their species then, collectively, the framework will have high explanatory power. Even with such explanatory capability, however, predictive power does not automatically follow. The ability to predict depends on the similarity between pieces of the jigsaw. If, for instance, large size has always predisposed species to extinction, we might claim (at least provisionally) a general principle. But if the effect of size has varied through time, among taxa and among causal processes, it indicates that size interacts with some other factor or factors. The more interactions there are, the harder it will be to go from explanation to prediction.

In this paper, we review the theory predicting which traits might matter, and then consider the progress so far in putting the jigsaw together and the search for commonalities—a search in which conservation biologists and evolutionary biologists are joining forces. Before that, however, we address the formidable problems of evidence that hamper both individual studies and, more especially, comparisons among them.

## Problems of evidence

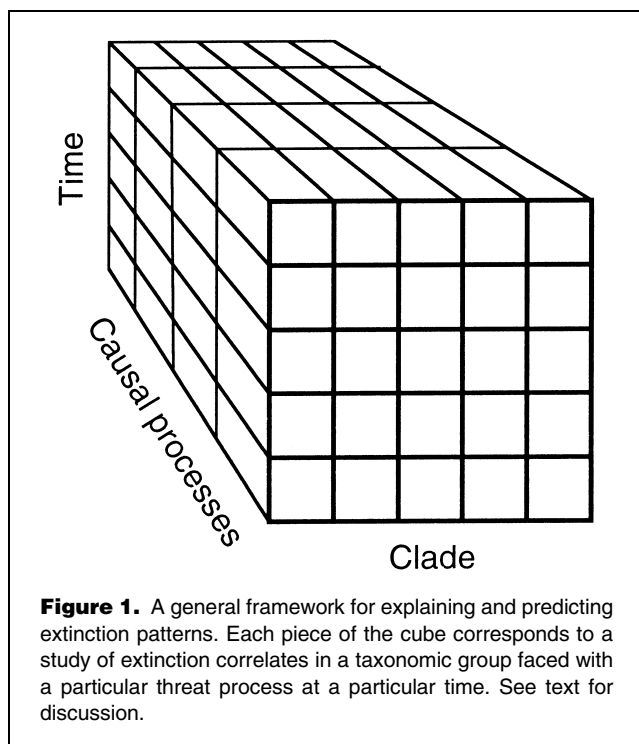
The first difficulty to be faced when looking at species extinction is deciding exactly what species are. Alarming,

<sup>1</sup>Department of Biology, Imperial College, Ascot, UK.

<sup>2</sup>Zoological Society of London, Regent's Park, London.

Funding agency: Natural Environment Research Council (NERC)—Grant Numbers: GR3/11526 and GR8/04371.

\*Correspondence to: Andy Purvis, Department of Biology, Imperial College, Silwood Park, Ascot, Berkshire, SL5 7PY. E-mail: a.purvis@ic.ac.uk



there are over 20 species concepts in current use.<sup>(7)</sup> For instance, many neontologists (i.e., biologists studying living species) favour the biological species concept, in which species are groups of organisms that can breed only within the group. This concept is appealing because the species are separate evolutionary lineages. Paleontologists have no way of assessing breeding group status, so have to use a species concept based on morphology—species have to look different, but might not be separate lineages. With different workers using such different concepts that some are uneasy about even using the word “species”,<sup>(8)</sup> it would seem that any attempt to make comparisons among species, groups or between past and present is doomed. Most biologists, however, whether studying living organisms or fossils, have a rather similar view of what “species” means. They probably have little difficulty with a theoretical species concept something like “a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley’s (Ref. 9) evolutionary species concept). The arguments mostly concern decisions on whether organisms in a sample are or are not members of the same species.<sup>(7)</sup> The different ways of deciding sometimes give different answers and all will lead to mistakes, but since they are mostly aiming at basically the same concept, then comparison among studies is reasonable. Comparisons are made even easier by the fact that biologists nearly always base species decisions on morphological similarity and difference,<sup>(10)</sup> In addition, pa-

leontologists and neontologists often have similar views about the degree of difference that corresponds to the species boundary.<sup>(11,12)</sup> The phylogenetic species concept, however, does pose a problem in that it can lead to “species inflation” and overestimation of extinction rates for the modern biota.<sup>(13)</sup> None of the neontological studies that we discuss below have this problem.

Extinction is conceptually simple—a species is extinct when its last member has died—but paleontologists and neontologists each face difficulties in measuring extinction rates in practice. The most fundamental problem for paleontologists is that, for most groups and times, the fossil record is too incomplete to be analysed at the species level—perhaps 1% of extinct species are known as fossils<sup>(14)</sup>—so higher taxa such as families are the units of analysis. These taxa are not comparable evolutionary units among major groups.<sup>(15)</sup> With a good record, extinction rates can be estimated as the reciprocal of species’ durations,<sup>(16)</sup> which in turn can be estimated from species’ patterns of fossil occurrence through time.<sup>(17,18)</sup> Such a process will surely underestimate typical species extinction rate, though, because the species that have left a fossil record are a very biased sample in that they would have had on average unusually big geographic ranges, many individuals and long durations.<sup>(11)</sup> A final problem is “pseudoextinction”: a species’ stratigraphic range stops not because of extinction but because it has changed into a form with a different name. Each of these three problems is likely to matter less when comparing closely related taxa, as any biases are more likely to be similar for them than for taxa across the whole sweep of life.

Neontologists face difficulties in identifying species extinctions. Many candidate species for extinctions are poorly known with restricted distributions in remote areas so their actual status is hard to determine. For example, IUCN (the World Conservation Union) requires evidence that the species habitat has been well and appropriately surveyed without any sign of the species.<sup>(19)</sup> This definition is sure to under-record extinctions—perhaps appropriately since conservation resources will not be forthcoming for species listed as extinct. Our best evidence on recent extinctions comes from information on birds and mammals over the last 500 years,<sup>(20,21)</sup> but even lists of such well-studied taxa are sure to be very incomplete. To move beyond documenting individual cases to investigate general extinction trends, we have to use less direct methods. One is to use information in threatened species lists (e.g. Ref. 19), with the assumption that these species are appropriately classified and therefore represent the next wave of extinctions.<sup>(22)</sup> Such lists are particularly useful when based upon comprehensive surveys of entire higher taxa or regions. This completeness permits, if good natural history data are also available, fine-grained matched-pairs comparisons between threatened and non-threatened species. Many more independent comparisons can be made

at the species level than at the higher levels generally available to paleontologists, giving greater statistical power.

### Reasons for extinction

Species are lost from a system either through perturbations imposed on it from outside (extrinsic causes, which may be biotic or abiotic) or because of evolutionary changes in its members (intrinsic causes). What traits might favour extinction under each of these scenarios? A null possibility would be that no traits are important, and that extinction is just a “hail of bullets”,<sup>(23)</sup> extirpating species at random. As we shall see, extinction is typically not random in this sense: it often affects some taxa more than others, a phenomenon known as selectivity.<sup>(24)</sup> Another meaning of “random” is harder to discount, however, especially for extrinsic perturbations. If a biota is suddenly faced with a radically different selective regime from its previous one, then survival can be a matter of luck: what matters is how well the species’ phenotype fits the new environment.<sup>(25–27)</sup> The pattern of survival is statistically nonrandom—related species, with similar adaptations, will share a common fate—but evolutionarily random.<sup>(28)</sup> Rejection of evolutionary randomness requires demonstration that the same traits have been associated with extinction time and time again. Theory leads to some predictions of which might be relevant.

Specialization has been linked to extinction-proneness for over a century.<sup>(29)</sup> The logic is certainly very reasonable. When the environment changes, species with broad tolerances are more likely to be able to persist than are those with narrow or fragile niches. However, objective definition is extremely difficult.<sup>(30)</sup> specialization is in the eye of the beholder. “Specialists” have sometimes been identified in ways that prevent any useful conclusions: by their oddness (automatically making “generalists” dominant), by the poorness-of-fit of their adaptations to their environment (making any conclusions circular), or because they possess derived characters (species tend to). More reasonable definitions are based on the breadth of species’ tolerances, but usually only one or a few aspects of niche breadth are considered. This may be a problem, as most species will have broad tolerances along some niche “axes” but narrow tolerances in others. Again, comparisons between closely related taxa are likely to be the most insightful, as they are likely to have similar tolerances on many of the unmeasured “axes”.

Bearing this in mind, there are several traits that can be viewed as specializations likely to increase extinction rate by restricting species’ niche breadth: high trophic level, limited powers of dispersal and small geographic range.<sup>(31–33)</sup> Perhaps the strongest prediction is for species depending upon other particular species: host-specific parasites must have extinction rates at least as high as their hosts,<sup>(34)</sup> for instance, and plants with specific pollinators or dispersers are in a parallel situation.<sup>(35,36)</sup>

Intrinsically caused extinctions are examples of “Red Queen” evolution,<sup>(37)</sup> which supposes that species within a system are engaged in a dynamic zero-sum game. Selection works within each species to improve its fitness relative to the others; extinction is the price of failing to keep up with the changes in the biotic environment. Under this model, the rate at which populations can adapt is likely to be crucial to their long-term survival. Two problems complicate tests of this simple proposition. Firstly, observed rate of evolution—which can be measured from comparative data<sup>(38)</sup>—is not a direct measure of the ability to evolve, because it is confounded by the past intensity of selection (about which we will usually know nothing). We cannot strongly infer that lineages that evolved slowly could never have evolved rapidly. Secondly, there is a surprising amount of uncertainty about how population size and structure affect evolvability. If populations are reduced to small size—a genetic bottleneck—and kept small for many generations, genetic variability is rapidly lost to drift. But how large must populations be for new mutations to arise quickly enough to replace the lost variation? An effective population size of 500 was proposed initially;<sup>(39)</sup> more recently, 5000 has been suggested.<sup>(40)</sup> The debate continues, with key points of contention including (1) the rate at which non-deleterious mutations arise, (2) the extent to which “deleterious” mutations provide evolutionary potential in changing environments, and (3) how conservative to be when faced with such uncertainties.<sup>(41–43)</sup> Another ongoing debate concerns whether population subdivision enhances the rate of adaptation, as proposed by Wright.<sup>(44)</sup> Recent supporting evidence<sup>(45,46)</sup> has been refuted;<sup>(47,48)</sup> the question remains open.<sup>(49)</sup>

Two predictions, though, can be made about correlates of evolvability. The first is that maximal evolutionary rates will correlate inversely with generation time, because of a strong dependency of the mutation rate on generation time. The second is that sexual populations can generally adapt more rapidly than asexual ones: favourable mutations can be united by recombination, and have a very much greater chance of becoming fixed.<sup>(50)</sup>

Asexual populations are at another disadvantage. As well as low rates of adaptation, asexual populations are more prone to maladaptive changes.<sup>(51)</sup> Recombination permits more efficient purging of deleterious mutations than is possible in asexual lineages, and drift can lead to the iterative loss of the currently fittest genotype. These are not the only circumstances in which successive generations are predicted to become increasingly extinction-prone. Under a recent population dynamic model,<sup>(52)</sup> intraspecific competition causes highly adapted character traits to evolve. If trait fitness is frequency-dependent then an increase in mean individual competitive ability can decrease the absolute fitness of all individuals in the population. Under these conditions, an increase in mean trait value leads to reductions in population

**Table 1.** Extinction patterns of nine different major marine invertebrate taxa after five mass extinction events

Mass extinction event (millions of years before present)	Mean extinction severity for event (no. families extinct/ no. extant)	Casualties	Survivors
Late Ordovician (455 M yr)	0.21 (65/310)	Crinozoans Cephalopods	Poriferans Foraminifera Gastropods
Late Devonian (370 M yr)	0.21 (68/322)	Cephalopods Poriferans Ostracodes	Bryozoans Foraminifera Gastropods
Late Permian (255 M yr)	0.63 (220/348)	Crinozoans Anthozoans Brachiopods Bryozoans	Foraminifera Poriferans Bivalves Gastropods
Late Triassic (220 M yr)	0.10 (18/178)	Cephalopods	Crinozoans Bryozoans Ostracodes Poriferans
Late Cretaceous (75 M yr)	0.11 (46/425)	Cephalopods Poriferans	Crinozoans Anthozoans

Extinction severity is measured as the number of families extinct/number extant in each taxon at the end of the extinction event. Only those groups whose severities were significantly different from the mean at each event are shown. Modified from ref. 24 and based on an analysis of Sepkoski's (1982) database of the stratigraphic ranges of marine invertebrate families.

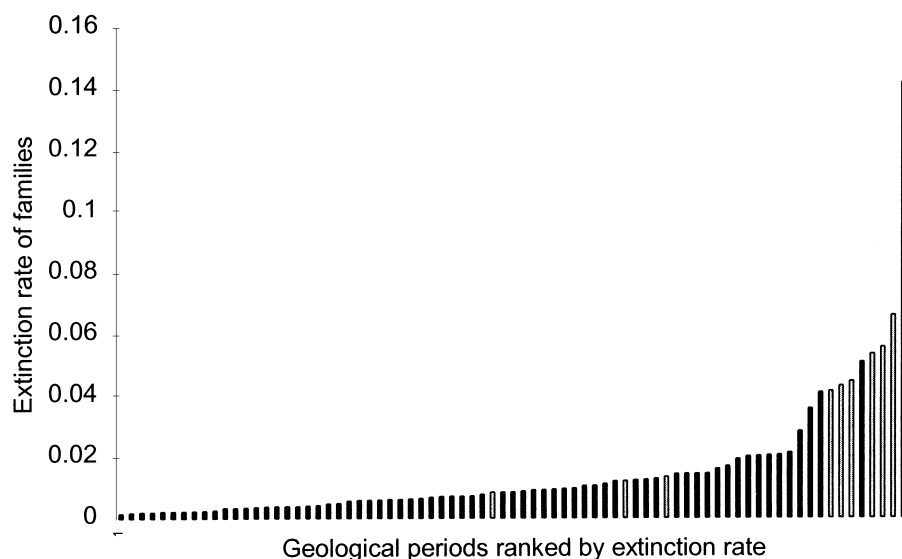
sizes and increases the probability of a species-level extinction in a variable environment.

### Extinction patterns

The intensity of extinction has varied enormously through geological time. At least five “mass extinctions” are generally recognised (Table 1)—events that have wiped out a significant proportion of the world's biota in a geologically insignificant period of time.<sup>(53)</sup> By far the most severe was the event at the end of the Permian. Over 50% of taxonomic families, 80% of genera and perhaps 95% of species disappeared at that time. The late Permian event is the most striking among the “Big Five”, but the other four have been closely documented and extrinsic causes sought to explain them.<sup>(53)</sup> The Permian event, which lasted about five to eight million years, appears to have been associated with massive global changes in physical structure that were, on a geological time scale, rapid. These included the formation of the new continent of Pangaea and associated tectonic activity, climate change and sea-level changes. The mass extinction at the end of the Cretaceous, during which many marine invertebrates and reptiles as well as terrestrial vertebrates and plants disappeared, is believed to have been caused by climate change resulting from an extraterrestrial impact. Observations of more-or-less contemporaneous events in the past can rarely be used to determine cause and effect but, at least for these cases, there seems compelling evidence that the habitats of the victims were exposed to highly unusual levels and rates of alteration of external conditions. Similar causes have been sought and

documented for the other periods of mass extinction.<sup>(53,54)</sup> Very high rates of extinction have also been observed outside of the ‘Big Five’. Figure 2 ranks the extinction rate of families in each of 79 geological intervals (from data in Ref. 55). The “Big Five” are shaded light grey. Although these events are all towards the right-hand end of the graph, there is no clear discontinuity, and some intervals outside mass extinctions also show these high rates. There are many methodological difficulties with this approach, caused by averaging extinctions over entire intervals when they may actually have occurred during only a relatively short part of the time, and by taking account of the overall diversity during the entire interval.<sup>(56)</sup> Nevertheless, the plot reveals a more or less continuous distribution of extinction intensities.

As Table 1 indicates, the “Big Five” were all highly selective, hitting some groups much harder than others.<sup>(23,24,53,57)</sup> Despite their huge influence, these events are responsible for perhaps 10% of all species extinctions. Most species die out at during periods of so-called “background” extinction. Here, too, different groups are affected at different rates: per-species extinction rates vary significantly among major groups.<sup>(37,58)</sup> The current crisis is also highly selective. The highest prevalences of extinction risk among major extant groups are found in fishes, amphibians, reptiles and mammals (once the comprehensiveness of assessment is accounted for).<sup>(19,59)</sup> There is also great variability in risk levels among groups at lower taxonomic levels.<sup>(60–63)</sup> For example, Polynesian land snails of the family Partulidae have over 100 species almost all of which are now critically endangered or extinct as a result of



**Figure 2.** Ranked extinction rates of taxonomic families for the geological intervals of the Phanerozoic. Extinction rate is measured as the proportion of families going extinct in each interval divided by the interval's length. Note that due to biases resulting from both the family diversity and inaccuracies resulting from the estimated length of the intervals this measure of extinction rate, as well as other possibilities, may be misleading.<sup>(56)</sup> The light-shaded bars are intervals containing the 'Big Five' mass extinctions. Data from the Web site based on Ref. 55, <http://palaeo.gly.bris.ac.uk/frwhole/FR2.html>.

the introduction of a predatory snail.<sup>(64)</sup> Hundreds of fish species from East African Rift Valley lakes are now extinct as a result of the introduction of the Nile perch<sup>(65)</sup> and mussels of the family Unionidae in the United States are severely threatened by pollution and exploitation.<sup>(66)</sup> The first generalization that can safely be made is that extinctions—past, present, and pending—are not statistically random.

If extinction is selective, what is it selecting? Can we identify the attributes of organisms that have led to their demise? Are they in accord with theoretical predictions, and are the patterns consistent among taxa, threatening processes and time periods? We now consider the progress so far in putting together the jigsaw outlined in the introduction (see also Fig. 1), before drawing the information together to assess the likely potential explanatory and predictive power of the framework. As discussed above, studies of the current extinction crisis, especially as it affects well-known groups like vertebrates, are likely to be a more statistically powerful and more comparable. We therefore start by focussing on these studies.

Studies on a range of vertebrate taxa have picked out correlations between extinction-proneness and traits that can be viewed as indicating restricted niche breadth: small geographic range, low population density, and high trophic level (Table 2). What is more, this pattern holds at different scales of analysis: local population extinctions and global species extinctions give broadly similar patterns. Vulnerability to local extinctions goes with low abundance, ecological specializa-

tions, large home range size and poor dispersal abilities.<sup>(67–71)</sup> Similarly, differences at equilibrium may be observed through comparisons of species on ecological “islands”—either true islands, montane islands or habitat islands which were once all part of a larger landscape<sup>(72–74)</sup> (Table 2). Here, differences in abundance and ecological specialization again contribute to population persistence in birds and reptiles at that local level. On the other end of the scale, studies of species vulnerability find associations with small geographical ranges, low abundance and high trophic level in both mammals and birds.<sup>(6,61,75)</sup> Carnivores, in a high trophic niche with only very narrow tolerances, are energetically “on the edge”.<sup>(76)</sup> There is evidence linking dietary specialization with extinction in other groups too. Bark beetles of the genus *Dendroctonus* differ in the proportion of available host plants that they utilise. The phylogenetic distribution of specialist bark beetles is significantly overdispersed, or “tippy”: they always have close relatives that are generalists, and they appear to have higher rates of extinction and/or lower rates of speciation.<sup>(77)</sup>

The phylogenetic distribution of asexuality is also “tippy”,<sup>(51,78)</sup> providing good evidence that rates of adaptation are important determinants of extinction vulnerability. Among some mammal and bird groups, long generation times, which limit the maximal rate of adaptation, are associated with high extinction risk (Table 2; but see below), and large body size is often positively correlated with both extinction-proneness and generation time. In the last 50,000 years, over 70% of large

**Table 2.** Summary of life history and ecological correlates of extinction in the present and the last 500 years in different animal taxa

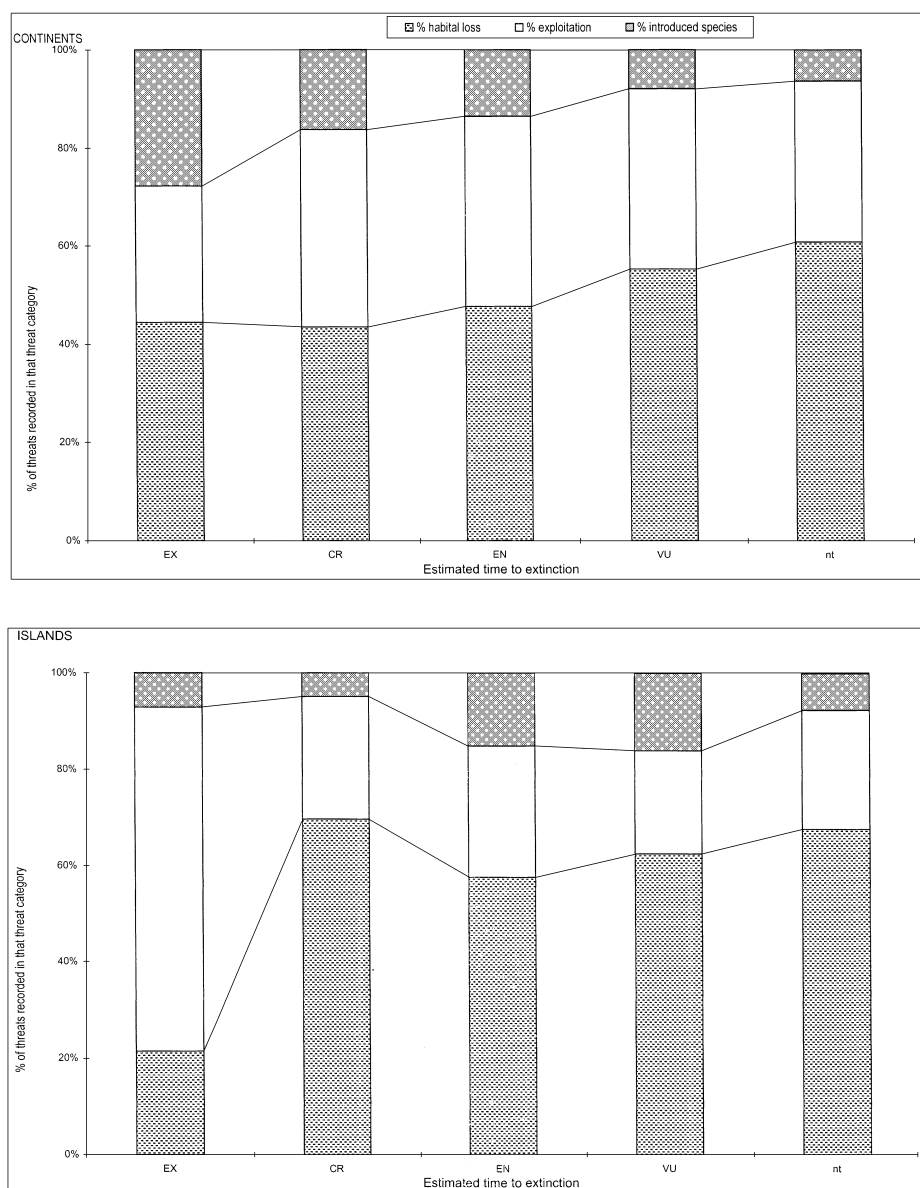
Extinction correlate	Direction of the correlation with extinction risk		
	Positive	Negative	No relationship
Geographic range		Primates <sup>g</sup> (6)* Carnivores <sup>g</sup> (6)* Birds <sup>g&amp;l</sup> (72, 73, 97, 98)*	
Home range	Carnivores <sup>l</sup> (71)* Primates <sup>l</sup> (4)		
Population density		Reptiles <sup>l</sup> (74)* Primates <sup>g</sup> (6)* Carnivores <sup>g</sup> (6)*	
Trophic level	Primates <sup>g</sup> (6)* Carnivores <sup>g</sup> (6)* Hoverflies <sup>g</sup> (77)		
Dietary specialization		Insects <sup>g</sup> (82)*	
Dispersal ability			Insects <sup>g</sup> (82)*
Habitat specialization	Reptiles <sup>l</sup> (74)* Birds <sup>g</sup> (81)* Primates <sup>g</sup> (99)		Birds <sup>g</sup> (81)*
Generation time	Carnivores <sup>g</sup> (6)* Birds <sup>g</sup> (61)* (81)*	Birds <sup>g</sup> (81)*	Primates <sup>g</sup> (6)* Reptiles <sup>l</sup> (74)* Hoverflies <sup>g</sup> (82)*
Body size	Primates <sup>g</sup> (100) (6)* Birds <sup>g&amp;l</sup> (72, 75) (73) (61)* (81)* Hoverflies <sup>g</sup> (82)*	Birds <sup>g&amp;l</sup> (72, 81)* All mammals <sup>g</sup> (21)	All mammals <sup>g</sup> (62) Carnivores <sup>g</sup> (6)* Reptiles <sup>l</sup> (74)*
Island living	All mammals <sup>g</sup> (21, 62)	Birds <sup>g</sup> (98)*	Primates <sup>g</sup> (6)* Carnivores <sup>g</sup> (6)*

Sources marked with an asterisk attempted to control for at least one possible confounding factor in their analyses (e.g. phylogenetic nonindependence, intercorrelated variables), g and l represent studies where extinction was measured as a global species extinction or a local population extinction, respectively. Reference numbers given in parentheses.

mammals in North America, South America and Australia died out, very probably because of human overexploitation,<sup>(79)</sup> interestingly, the extinction was less severe in Africa—where humans were an intrinsic part of the system rather than a sudden extrinsic force.<sup>(80)</sup>

However, Table 2 illustrates that not all taxa show the same patterns of correlation. Some studies show small body size and short generation time to correlate with high extinction risk.<sup>(72,81)</sup> Further, generation time is an important predictor of extinction in carnivores and birds but not in primates, reptiles or hoverflies. Similarly, body size is important in primates, birds and hoverflies but not in carnivores and reptiles.<sup>(6,61,74,82)</sup> Some of the discrepancies may result from a lack of statistical rigour. Many extinction studies do not control for associations between ecological and reproductive characters, nor for the non-independence of species data due to a shared phylogenetic history. Yet there can be complex interactions among the determinants of extinction<sup>(6,72,73)</sup> that need to be considered. However, even considering the more rigorous studies (highlighted with an asterisk in Table 2), no clear pattern emerges for traits pertaining to rate of adaptation in different taxa.

One possible explanation for some of the heterogeneity is that the patterns of correlation depend on the nature of the causal process<sup>(72,83)</sup>—another of the axes in Fig. 1. The processes responsible for recent and pending extinctions are often well understood: anthropogenic habitat loss, over-exploitation and invasive species are the major extinction driving processes. Recent mammal extinctions have been concentrated on islands and in Australia<sup>(20,21)</sup> and have tended to track patterns of human exploration and settlement. Explorers and early settlers tended to overexploit the larger-bodied species, and to bring domestic species and vermin, which threatened many of the endemic vertebrates.<sup>(84)</sup> Often these threats were accentuated as settlers cleared key habitat areas for habitation and agriculture—a trend that continues to this day. Introduced species may cause extinctions because they are superior competitors or predators, or bring disease and novel pathogens to which the naïve island endemics have no resistance. Processes that reduce habitat availability might be expected to most affect those species that are ecologically specialized, whereas processes such as human persecution and introduced predators may have more of an impact on



**Figure 3.** Likely changes over the time course in the impact of different threatening processes on continental and island mammals. Species are classified according to their IUCN threat category with the estimated time to extinction increasing from left to right. EX, Extinct; CR, Critically Endangered; EN, Endangered; VU, Vulnerable; nt, near threatened. From Ref. 85.

species with long generation times.<sup>(81)</sup> This expectation is borne out for birds,<sup>(81)</sup> showing that a knowledge of the threatening process can greatly improve our ability to explain the pattern of extinction.

The driving processes also change over time—the third axis in Figure 1—further confusing the pattern of extinction correlates. For example, most recent mammalian and avian extinctions have been of species restricted to islands, succumbing to overexploitation and introduced species.<sup>(21,62)</sup>

However, if threatened species lists are effective measures of future extinctions, and increasing threat level is used as a surrogate of time to extinction, then we expect to see increasing extinction in continental areas and caused by habitat loss<sup>(85)</sup> (Fig. 2). Additionally, among Mediterranean floras, the diversity and the proportion of threatened species decrease with the time since human occupancy.<sup>(86)</sup> Vulnerable species have presumably been already driven to extinction during the long period of human contact. Species

more prone to extinction may have already been filtered out of the system,<sup>(87)</sup> changing the pattern on which future extinction processes would now act. This limits the predictive power of any models, at least until all of the pieces of the extinction jigsaw are in place.

A key question is the extent to which traits promoting extinction in the current crisis are the same as those that operated in the geological past. Unfortunately, a definite answer is not yet possible for at least two reasons. First, paleontologists and neontologists studying global extinction have typically looked at different taxa. The best fossil data are mostly for various marine invertebrate groups,<sup>(88)</sup> whereas the best assessments for extinction risk of the present biota are for mammals and birds.<sup>(19)</sup> These different areas of study are even more problematic given the heterogeneity of pattern seen even within taxa (above). The second reason, alluded to earlier, is that most paleontological studies have very limited statistical potential because of the need to compare large groups: selectivity is much easier to demonstrate convincingly than to explain convincingly. Bearing that in mind, are there any hints of commonality?

Specialization, in various forms, is commonly linked with high extinction rates, as predicted by theory. At a time of background extinction, subclasses of Carboniferous crinoid species found in fewer habitat types had higher per-species extinction rates,<sup>(58)</sup> and a restricted diet breadth (hypercarnivory) is associated with shorter species durations in carnivorous mammals.<sup>(89)</sup> Marine invertebrate taxa with planktonic widely dispersing larvae and larger geographic ranges that were phylogenetically situated in species-rich clades had lower extinction rates than narrowly restricted species-poor taxa with non-planktonic larval stages.<sup>(90,91)</sup> The evidence suggests, in contrast, that the biotic characteristics that enhance survival during times of low extinction are largely ineffectual at times of mass extinction.<sup>(91)</sup> Even during such events, however, specialization is again implicated. Marine bivalve genera with narrow geographic ranges had lower extinction rates during the end-Cretaceous mass extinction than those with narrower tolerances.<sup>(91)</sup> Wide geographic ranges have also been important for survival at other mass extinction events (reviewed by Ref. 57). Additionally, generalist forms often dominate the fossil record in the succeeding intervals after extinction events.<sup>(54)</sup> Other traits in Figure 2 are only patchily implicated. Larger body size is sometimes (e.g., Ref. 92) but by no means always (e.g., Ref. 93) associated with short lifespan of species. The fossil record demonstrates that extinction has often been highly nonrandom, but has so far led to the identification of relatively few statistically convincing correlates of extinction rate.

### Emerging issues

Extinction is a selective process, inviting a search for the targets of selectivity. Species go extinct because their

adaptations no longer fit their environment, nearly always because the environment changes. Competitive inferiority, often cited as a reason for extinction, is usually the result of such a change—rather than a cause of extinction, it is an intermediate step. Much of the theory about which species go extinct concerns extinctions brought about by evolutionary change in interacting species—intrinsic changes, in our terms. However, intrinsically caused extinctions are hard to study. Virtually all extinctions happening currently are part of the anthropogenic—extrinsic—crisis. Moving to the fossil record, most lineages extirpated by ongoing coevolution seem likely to have been of short duration on a local scale, so may not even be detectable from the fossil record even if they make up the majority of extinctions. Thus it seems impossible to estimate the relative frequencies of intrinsically and extrinsically caused extinctions.

Extrinsic driving forces—geological change, climate change, faunal mixing and now anthropogenic disturbance—can swamp the effects of the smaller scale evolutionary processes. If the entire habitat of a species is eliminated, the adaptive potential of an organism may have little bearing on its ability to persist. To that extent, survival may well be a matter of luck,<sup>(26)</sup> the statistical nonrandomness of the extinction pattern notwithstanding.<sup>(28)</sup> Similarly, the extrinsic drivers vary with time and place and the subset of species that perish as a result of their actions will vary accordingly. This may explain why there are rather few common themes among the extinction-prone characteristics. While the explanatory model for the current crisis holds promise, hopes of a powerful predictive model should not be too high.

One commonly found correlate of extinction is specialization. Why does it keep evolving? Models all depend upon some cost to being a generalist,<sup>(30)</sup> whether that cost is in terms of being a “jack of all trades, master of none” or in failing to find a mate. The “jack of all trades” cost is particularly interesting, because it views specialization as a way of keeping up with, or getting an advantage over, the opposition. As such, specialization is successful Red Queen evolution—a way to avoid extinction—and therefore may not be a bad thing in systems free from extrinsic perturbations. In support of this view, the fossil record suggests that competitive replacement of one group by another is surprisingly uncommon, at least in tetrapods;<sup>(94)</sup> by contrast, ecological incumbency is a common, perhaps dominant, pattern.<sup>(95)</sup> Under this view, the lack of evidence for generalism as an extinction-promoting trait is ascribed to the difficulty, outlined above, of studying intrinsically caused extinctions.

Can we look through the lens of past extinctions to get a clearer picture of the present crisis? The differences in coarseness of grain, in the nature of evidence and in simply which groups are best studied all combine to make the lens rather opaque. The picture is improved if we recognise that the species extinction spasm that we face now will be situated at



the right-hand end of Figure 2. Both in terms of the extent and rate of diversity loss it will be a mass extinction. But, unlike the mass extinctions of the past, the driving processes are not attributable to abiotic geological changes or extraterrestrial impacts. Instead, the direct and indirect causes are almost entirely due to the activities of a vast, growing and global human population competing for natural resources with all the other species on earth. Some of the more direct impacts of people, such as over-exploitation and alien introductions, are undoubtedly selective. Certain species, such as those with relatively low reproductive potential or those that are naïve to predators or competitors will fare worse under such pressures. However, larger scale anthropogenic forces, such as the clearance of entire habitats or widespread climate change will be much less selective and we can expect there to be relatively few survivors. Accordingly, the survivors of the current extinction episode may not easily be deduced from the patterns seen in the past because the drivers are so different. Even over historical times, anthropogenic driving forces have varied in nature. During early periods of human population growth and settlement, species extinctions were largely a result of over-hunting; later civilisations spread non-indigenous species with the early explorers and today high population densities over most of the earth result in rapid habitat change as extensive areas are cleared for cultivation and settlement. In the future, we expect habitat changes and fragmentation to increase and to be accompanied by rapid climate change. How do we build this changing pattern of causation into our predictive models and how do we distinguish between the more and less selective processes?

Despite the difficulties outlined here, we believe that there are general patterns to be uncovered and that deducing them is a necessary step in improving our understanding of species extinctions. However, building this useful framework will require a more structured approach than the simple collation or meta-analysis of existing data. The analysis will need to recognise the different drivers and scales, and to focus explicitly on assemblages of species where there is comparable information about extrinsic driving processes as well as biological attributes. In this way, the relative importance of different driving processes, the life histories and ecologies of species, and their phylogenetic relationships—as well as the interactions between these—can all be controlled for and evaluated rigorously. There seems little prospect of doing this for periods way back in the fossil record, which in any case may have little relevance for the present because of the substantial differences in processes and taxonomic affinities. Some of the more recent fossil assemblages of larger vertebrates, however, are becoming well known and more comparable to contemporary studies of related taxa. Similarly, archaeological and historical studies are now revealing much more about how early human settlement impacted on species (e.g. Ref. 96).

Such an overarching approach has not yet been attempted, and it will be far from easy. Nonetheless we see such a framework as essential if we are to understand how and when extinctions occur, and to make the wealth of information that we have—from both present and past—contribute to our responsible management of the environment in which our own species now plays so dominant a role.

## Acknowledgments

Guy Cowlshaw, Rich Grenyer, Paul Harvey, Adam Wilkins, and an anonymous referee made comments that greatly improved the manuscript.

## References

1. May RM, Lawton JH, Stork NE. Assessing extinction rates. In Lawton JH, May RM, ed; *Extinction Rates*. Oxford: Oxford University Press. 1995. p 1–24.
2. McKinney ML. Branching models predict loss of many bird and mammal orders within centuries. *Anim Conserv* 1998;1:159–164.
3. Pimm SL, Russell GJ, Gittleman JL, Brooks TM. The future of biodiversity. *Science* 1995;269:347–350.
4. Harcourt AH. Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In Caro T. ed; *Behavioral Ecology and Conservation Biology*. New York: Oxford University Press. 1998. p 56–79.
5. Cowlshaw G, Dunbar RIM. *Primate Conservation Biology*. Chicago: Chicago University Press; 2000.
6. Purvis A, Gittleman JL, Cowlshaw G, Mace GM. Predicting extinction risk in declining species. *Proc R Soc Lond B* 2000;
7. Mayden RL. A hierarchy of species concepts: the denouement in the sage of the species problem. In Claridge MF, Dawah HA, Wilson MR. ed; *Species: The Units of Biodiversity*. London: Chapman and Hall; 1997. p 381–424.
8. Smith AB. *Systematics and the fossil record: documenting evolutionary patterns*. Oxford: Blackwell Scientific. 1994.
9. Wiley EO. The evolutionary species concept reconsidered. *Syst Zool* 1978;27:17–26.
10. Claridge MF, Dawah HA, Wilson MR. Practical approaches to species concepts for living organisms. In Claridge MF, Dawah HA, Wilson MR. ed; *Species: The Units of Biodiversity*. London: Chapman and Hall. 1997. p 1–15.
11. Erwin DH, Anstey RL. Speciation in the fossil record. In Erwin DH, Anstey RL. ed; *New Approaches to Speciation in the Fossil Record*. New York: Columbia University Press. 1995. p 11–38.
12. O'Keefe FR, Sander PM. Paleontological paradigms and inferences of phylogenetic pattern. *Paleobiol* 1999;25:518–533.
13. Knowlton N, Weigt LA. Species of marine invertebrates: a comparison of the biological and phylogenetic species concepts. In Claridge MF, Dawah HA, Wilson MR. ed; *Species: The Units of Biodiversity*. London: Chapman and Hall; 1997. p 199–219.
14. Raup DM. The role of extinction in evolution. *Proc Natl Acad Sci USA* 1994; 91:6758–6763.
15. Avise JC, Johns GC. Proposal for a standardized temporal scheme of biological classification for extant species. *Proc Natl Acad Sci USA* 1999; 96:7358–7363.
16. Stanley SM. *Macroevolution*. San Francisco: W H Freeman. 1979.
17. Foote M, Raup DM. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiol* 1996;22:121–140.
18. Marshall CR. Confidence intervals on stratigraphic ranges: partial relaxation of the assumptions of randomly distributed fossil horizons. *Paleobiol* 1994;20:459–469.
19. Baillie JEM, Groombridge B. *IUCN Red List of Threatened Animals*. Gland. Switzerland: IUCN. 1996.
20. Groombridge B. *Global Biodiversity: Status of the World's Living Resources*. London: Chapman & Hall. 1992.

21. MacPhee RDE, Flemming C. *Requiem Aeternam*: the last five hundred years of mammalian species extinctions. In MacPhee RDE, ed. *Extinctions in Near Time: Causes, Contexts, and Consequences*. New York: Kluwer Academic/Plenum Publishers; 1999. p 333–371.
22. Mace GM. Classification of threatened species and its role in conservation planning. In Lawton JH, May RM, ed. *Extinction Rates*. Oxford: Oxford University Press; 1995. p 197–213.
23. Raup DM. *Extinction: Bad Genes or Bad Luck?* New York: Norton. 1991.
24. McKinney ML. Taxonomic selectivity and continuous variation in mass and background extinctions of marine taxa. *Nature* 1987; 325:143–145.
25. Jablonski D. Evolutionary consequences of mass extinction. In Raup DM and Jablonski D ed. *Patterns and Processes in the History of Life*. Berlin: Springer-Verlag. 1986. p313–329.
26. Gould SJ. *Wonderful Life: The Burgess Shale and the Nature of History*. New York: Norton. 1989.
27. Jablonski D. Mass extinctions: persistent problems and new directions. *Geological Society of America Special Paper* 1996;307:1–9.
28. Eble GJ. On the dual nature of chance in evolutionary biology and paleobiology. *Paleobiol* 1999;25:75–87.
29. Cope ED. *The primary factors in organic evolution*. Chicago: Open Court Publishing Co. 1896.
30. Futuyma DJ, Moreno G. The evolution of ecological specialization. *Ann Rev Ecol Syst* 1988;19:207–233.
31. Diamond JM. “Normal” extinctions of isolated populations. In Nitecki, MH, ed; *Extinctions*. Chicago: Chicago University Press. 1984. p 191–246.
32. Brown JH. *Macroecology*. Chicago: Chicago University Press. 1995.
33. McKinney ML. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Ann Rev Ecol Syst* 1997;28:495–516.
34. Stork NE, Lyal CHC. Extinction or “co-extinction” rates. *Nature* 1993;366:307.
35. Bond WJ. Assessing the risk of plant extinction due to pollinator and disperser failure. In Lawton JH, May RM, ed. *Extinction Rates*. Oxford: Oxford University Press; 1995. p 131–146.
36. Kevan PG. Pollinators as indicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems and Environment* 1999;74:373–393.
37. Van Valen L. A new evolutionary law. *Evolutionary Theory* 1973;1: 1–30.
38. Webster AJ, Purvis A. Ancestral states and evolutionary rates of continuous characters. In MacLeod N, Forey P, ed. *Morphology, Shape and Phylogenetics*. Taylor & Francis; in press.
39. Soulé ME. Thresholds for survival: maintaining fitness and evolutionary potential. In Soulé ME, Wilcox BA, ed. *Conservation biology: an evolutionary-ecological perspective*. Sunderland, MA: Sinauer; 1980. p 151–169.
40. Lande R. Mutation and conservation. *Conserv Biol* 1995;9:782–791.
41. Franklin IR, Frankham R. How large must populations be to retain evolutionary potential? *Anim Conserv* 1998;1:69–70.
42. Lynch M, Lande R. The critical effective size for a genetically secure population. *Anim Conserv* 1998;1:70–72.
43. Frankham R, Franklin IR. Response to Lynch and Lande. *Anim Conserv* 1998;1:73.
44. Wright S. The roles of mutation, inbreeding, outbreeding, cross-breeding and selection in evolution. *Proc Sixth Int Congress Genet* 1932;1:356–366.
45. Wade MJ, Goodnight CJ. Wright's shifting balance theory: an experimental study. *Science* 1991;253:1015–1018.
46. Peck SL, Ellner SP, Gould F. A spatially explicit stochastic model demonstrates the feasibility of Wright's shifting balance theory. *Evolution* 1998;52:1834–1839.
47. Coyne JA, Barton NH, Turelli M. A critique of Sewall Wright's shifting balance theory of evolution. *Evolution* 1997;51:643–671.
48. Coyne JA, Barton NH, Turelli M. Is Wright's shifting balance process important to evolution? *Evolution* 2000;54:306–317.
49. Peck SL, Ellner SP, Gould F. Varying migration and deme size and the feasibility of the shifting balance. *Evolution* 2000;54:324–327.
50. Peck JR. A ruby in the rubbish: beneficial mutations, deleterious mutations and the evolution of sex. *Genetics* 1994;137:597–606.
51. Judson OP, Normark BB. Ancient asexual scandals. *Trends Ecol Evol* 1996;11:A41–A46.
52. Matsuda H, Abrams PA. Runaway evolution to self-extinction under asymmetrical competition. *Evolution* 1994;48:1764–1772.
53. Hallam A, Wignall PB. *Mass Extinctions and their Aftermath*. Oxford: Oxford University Press. 1997.
54. Erwin DH. The end and the beginning: recoveries from mass extinction. *Trends Ecol Evol* 1998;13:344–349.
55. Benton MJ. *The Fossil Record 2*. London: Chapman & Hall. 1993.
56. Benton MJ. Diversification and extinction in the history of life. *Science* 1995;268:52–58.
57. Jablonski D. Extinctions in the fossil record. In Lawton RH, May RM, ed; *Extinction Rates*. Oxford: Oxford University Press. 1995. p 25–44.
58. Kammer TW, Baumiller TK, Ausich WJ. Evolutionary significance of differential species longevity in Osagean-Meramecian (Mississippian) crinoid clades. *Paleobiol* 1998;24:155–176.
59. TNC. *Priorities for conservation: 1996 annual report card for US plant and animal species*. 1996.
60. Russell GJ, Brooks TM, McKinney MM, Anderson CG. Present and future taxonomic selectivity in bird and mammal extinctions. *Conserv Biol* 1998;12:1365–1376.
61. Bennett PM, Owens IPF. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc R Soc Lond B* 1997;264:401–408.
62. Mace GM, Balmford A. Patterns and processes in contemporary mammalian extinction. In Entwistle A, Dunstone N, ed; *Future Priorities for the Conservation of Mammalian Diversity*. Cambridge: Cambridge University Press. 2000.
63. Purvis A, Agapow P-M, Gittleman JL, Mace GM. Nonrandom extinction risk and the loss of evolutionary history. *Science* 2000;288:328–330.
64. Mace GM, Peace-Kelly P, Clarke D. An integrated conservation programme for the tree snails of Polynesia (Partulidae): a review of captive and wild elements. *J Conchology* 1998.
65. Witte F, Goldschmidt T, Goudswaard P, Ligtoevet W, van Oijen M, Wanink J. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands J Zool* 1992;42:214–232.
66. Williams J, Warren M, Cummings J, Neves R. Conservation status of freshwater mussels in the United States and Canada. *Fisheries* 1992;18:6–22.
67. Bolger DT, Alberts AC, Soulé ME. Occurrence patterns of bird species in habitat fragments: sampling, extinction and nested species subsets. *Am Nat* 1991;137:155–166.
68. Terborgh J, Winter B. Some causes of extinction. In Soulé ME, Wilcox BA, ed; *Conservation Biology: An Evolutionary and Ecological Perspective*. Sunderland MA: Sinauer. 1980. p 119–133.
69. Newmark WD. Tropical fragmentation and the extinction of understorey birds in the Eastern Usambara mountains. *Conserv Biol* 1991;5:67–78.
70. Laurance WF. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv Biol* 1991;5:80–89.
71. Woodroffe R, Ginsberg JR. Edge effects and the extinction of populations inside protected areas. *Science* 1998;280:2126–2128.
72. Pimm SL, Jones HL, Diamond JM. On the risk of extinction. *Am Nat* 1988;132:757–785.
73. Tracy CR, George TL. On the determinants of extinction. *Am Nat* 1992;139:102–122.
74. Foutopoulos J, Ives AR. Reptile extinctions on land-bridge islands: Life-history attributes and vulnerability to extinction. *Am Nat* 1999;153:1–25.
75. Gaston KJ, Blackburn TM. Birds, body size, and the threat of extinction. *Phil Trans R Soc Lond B* 1995;347:205–212.
76. Carbone C, Mace GM, Roberts SC, Macdonald DW. Energetic constraints on the diet of terrestrial carnivores of differing body size. *Nature* 1999;402:286–288.
77. Kelley ST, Farrell BD. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). *Evolution* 1998;52:1731–1743.
78. Van Valen L. Group selection, sex, and fossils. *Evolution* 1975;29:87–94.
79. Martin PS. Catastrophic extinctions and the Late Pleistocene blitzkrige. In Nitecki NH, ed; *Extinctions*. Chicago: Chicago University Press. 1984. p 153–189.

80. Martin PS. Prehistorical overkill: the global model. In Martin PS, Klein RG, ed; *Quaternary Extinctions: A Prehistoric Revolution*. Tucson, Arizona: University of Arizona Press. 1984.
81. Owens IPF, Bennett PM. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc Natl Acad Sci USA* submitted;
82. Sullivan MS, Gilbert F, Rotheray G, Creasdale S, Jones M. Comparative analysis of correlates of Red data book status using European hoverflies (Diptera: Syrphidae). *Anim Conserv* 2000;3:91–95.
83. Lawton JH, May RM. *Extinction Rates*. Oxford: Oxford University Press. 1995.
84. Olson SL, James HF. Fossil birds from the Hawaiian Islands; evidence for wholesale extinction by man before western contact. *Science* 1982;217:633–635.
85. Balmford A, Mace GM, Ginsburg J. Challenges to conservation in a changing world. In Mace GM, Balmford A, Ginsburg J, ed; *Conservation in a Changing World*. Cambridge: Cambridge University Press. 1998. p 1–28.
86. Greuter W. Extinctions in Mediterranean areas. In Lawton JH, May RM, ed; *Extinction Rates*. Oxford: Oxford University Press. 1995. p 88–97.
87. Balmford A. Extinction filters and current resilience; the significance of past selection pressures for conservation biology. *Trends Ecol Evol* 1996;11:193–196.
88. Sepkoski JJ. Phylogenetic and ecological patterns in the Phanerozoic history of marine biodiversity. In Eldredge N, ed; *Systematics, Ecology and the Biodiversity Crisis*. New York: Columbia University Press. 1992. p 77–100.
89. Van Valkenburgh B. Major patterns in the history of carnivorous mammals. *Ann Rev Earth Planet Sci* 1999;27:463–493.
90. Jablonski D. Background and mass extinctions: the alteration of macroevolutionary regimes. *Science* 1986; 231:129–133.
91. Jablonski D, Raup DM. Selectivity of end-Cretaceous marine bivalve extinctions. *Science* 1995;268:389–391.
92. Stanley SM. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. *Paleobiol* 1986;12:89–110.
93. Jablonski D. Body size and macroevolution. In Jablonski D, Erwin DH, Lipps JH, ed; *Evolutionary Paleobiology*. Chicago: University of Chicago Press. 1996. p 256–289.
94. Benton MJ. Testing the roles of competition and expansion in tetrapod evolution. *Proc R Soc Lond B* 1996;263:641–646.
95. McKinney ML. Biodiversity dynamics: niche preemption and saturation in diversity equilibria. In McKinney ML, Drake JA, ed; *Biodiversity Dynamics*. New York: Columbia University Press. 1999. p 1–16.
96. Haynes G, Eiselt S. The power of Pleistocene hunter-gatherers: forward and backward searching for evidence about mammoth extinction. In MacPhee RDE, ed. *Extinctions in Near Time: Causes, Contexts, and Consequences*. New York: Kluwer Academic/Plenum Publishers; 1999. p 71–94.
97. Gaston KJ, Blackburn TM. Conservation implications of geographic range size-body size relationships. *Conserv Biol* 1996;10:638–646.
98. Manne LL, Brooks TM, Pimm SL. Relative risk of extinction of passerine birds on continents and islands. *Nature* 1999;399:258–261.
99. Jernvall J, Wright PC. Diversity components of impending primate extinctions. *Proc Natl Acad Sci USA* 1998;95:11279–11283.
100. Walker AC. Patterns of extinctions among the subfossil Madagascan lemuroids. In Martin PS, Wright HEJ, ed; *Pleistocene extinctions*. New Haven: Yale University Press. 1967. p 425–432.