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Ecological avalanches and the two kinds of extinction

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ABSTRACT

The patterns, causes and consequences of the extinction of species observable today differ from those chronicled in the fossil record. An evaluation of mechanisms of extinction and interpretation of the empirical evidence lead me to argue that competition, predation, invasion and habitat loss – the chief agencies responsible for ecological change and the extinction of species in the human-dominated biosphere today – occur on a relatively small scale, yield few collateral extinctions, and have until now led to species losses mainly among island and lake endemics. By contrast, I argue that the major and minor crises of the geological past were initiated by conditions inhibiting photosynthesis, and that starvation and habitat loss triggered by these conditions led to widespread collateral extinction of species. Conditions traditionally identified by palaeontologists as initiating mass extinction – oxygen deprivation, oversupply of nutrients and poisoning (by carbon dioxide, methane and sulphides) – are interpreted here as manifestations of the ecological avalanche triggered by a crisis among primary producers, and are therefore considered consequences rather than primary causes of extinction. The global trend for habitats to become more island-like and for highly productive environments to be heavily exploited, modified or even eliminated by human activity means that species on larger land masses and in the ocean will become increasingly vulnerable to biological causes of extinction and to further habitat loss. To reduce the biosphere's vulnerability to the kinds of extinction-generating avalanches chronicled in the fossil record, it is essential to protect species and biogeochemical processes in large, highly productive ecosystems.

Keywords: cascades, extinction, invasion, palaeontology.

INTRODUCTION

Extinction is a recurrent phenomenon in the history of life and in our own time. Ecologists grappling with the causes and consequences of extinction and looking for remedies to abate further losses have often pointed to the dramatic, long-term disruptions associated with the mass extinctions of the geological past as descriptive scenarios for the loss of species and the dismantling of ecosystems today. The underlying assumption is that past extinctions and their consequences are like present-day extinctions. By the same token, palaeontologists have sometimes taken the phenomenology of extinction in our own time as a guide to unravelling the mysteries of the great crises of the past.

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Parallels and differences between the human-caused extinctions of today and the crises of the geological past have received little analytical attention. Jablonski (1995, 2001) noted that species with narrowly circumscribed geographic ranges are vulnerable to extinction both today and during ‘normal’ (or ‘background’) times in the prehuman past, but he pointed out that the magnitude (or intensity) of extinction in the human-dominated biosphere falls well below that during the great geological crises. Nonetheless, the overwhelming opinion among scientists and the public is that human-caused extinction is, or soon will be, as devastating as were the geological mass extinctions (Ehrlich and Ehrlich, 1981; May *et al.*, 1995; Myers, 1997; Myers and Knoll, 2001).

Although extinction is clearly a process and outcome that is strongly affected by geography, ecology and the demographic characteristics of species, the full environmental context in which extinction and its aftermath take place has been largely ignored in most previous studies. Conservationists and palaeontologists alike typically think of extinctions and individual species as separate, independent occurrences, even if a common cause – a celestial collision, sea-level change, habitat fragmentation or arrival of a predator – is held to be responsible. Similarly, we have known for a long time that extinction is selective, but the implications of that selectivity have been left largely unexplored. For example, large mammals have shorter species longevities and suffer a generally higher risk of extinction than do small-bodied mammals (Van Valen, 1975; Diamond, 1984; Martin, 1984; Van Valkenburgh, 1999). Island species are more vulnerable than mainland species (Diamond, 1984; May *et al.*, 1995; Steadman, 1995). Large geographic ranges confer resistance to extinction on species during ‘normal’ times and on more inclusive clades during mass extinctions (Jablonski, 1986, 1995, 2001). These and many other patterns of selectivity that distinguish surviving from extinct lineages arise from factors that cause extinction in the first place, and have consequences that depend on how the species in question interact with other members of the ecosystems that the species occupied and forged. But these issues have not received much attention. Instead, extinction too often has stayed within the realm of phenomenological description. It has not entered the realm of theory based on first principles of causes, feedbacks and long-term effects set in a context of whole ecosystems.

My purpose in this paper is to identify and classify the fundamental causes of extinction, to show how these causes dismantle ecosystems, and to ascertain whether and how the elimination of particular species places other species at risk of extinction. I argue that top-down causes – the gain or loss of consumer species – together with habitat shrinkage and fragmentation are responsible for species losses and ecological disruptions in the human-dominated biosphere thus far, and that the resulting extinctions are different in character from, and less disruptive than, the regional to global bottom-up interruptions in photosynthesis that I suggest were responsible for most of the large and small crises earlier in Earth history. By clarifying how species losses propagate through ecosystems, this classification highlights the importance of protecting productive environments and of preventing the further fragmentation of the biosphere, a process that exposes the world biota to increasing risks of both top-down and bottom-up disruption.

THE CAUSES OF EXTINCTION

A species becomes extinct when conditions overwhelm the adaptive capacity of all its individuals. This happens either when all individuals die without producing offspring or more gradually when the death rate consistently exceeds the birth rate throughout the species range. If the severity, reach and duration of a crisis allow some individuals to survive and to leave offspring, the species undergoes range contraction, range shift or fragmentation, with the possibility that descendants become adapted to the new order. Persistence, therefore, depends on one or more of the following conditions: (1) the presence of refuges; (2) the ability to modify environments or to track environments to which the species was adapted before the crisis; and (3) the ability to adapt to the inclement conditions or their aftermath. If such accommodation and adaptation are impossible, the species will become extinct.

Unprecedented conditions and the extinctions they trigger may unleash collateral extinctions through the initiation of ecological avalanches or cascades. They do so by disrupting patterns of interaction and dependence among species. As one species (or a class of species) disappears, perpetuation of other species becomes impossible, resulting in collateral extinction. In an analysis of short-term experimental studies in which ecosystem responses to the elimination of species were monitored, Duffy (2003) showed that the elimination of powerful consumers (especially large-bodied, warm-blooded vertebrate grazers and predators, and large marine consumers) has generally far more dramatic effects on species composition and biomass than the removal of a species of primary producer. The implication of his analysis not explored by Duffy is that collateral extinction is potentially greater when consumers of large effect are eliminated than when plant species are withdrawn. The validity of this implication hinges on whether the pattern of loss reflects what happens in nature during crises.

The extent to which collateral extinction – that is, the length and severity of avalanches – occurs depends on: (1) how disruption arises; (2) on the reach (spatial extent) of the disturbance relative to the size of affected ecosystems and populations; (3) redundancy (whether the losses of habitats and species are reversible or replaceable); and (4) connectedness (the number and strengths of links connecting species within the ecosystem exposed to the disturbance). Removal of a species by extinction severs links. If the eliminated species provided a crucial good or service to other species in the community, those affected species will be exposed to a higher risk of collateral extinction. That risk is low, however, if the severed links can be replaced by links with other surviving species. Collateral extinction should therefore be widespread when one or more links crucial to the persistence of a species are broken and not replaced.

Disturbances interfere with life and potentially cause extinction in two non-exclusive ways: (1) through competition, predation or disease – a top-down effect imposed by enemy species; and (2) incapacitation of metabolism – a bottom-up effect expressed as interruptions in the supply of energy or food or as poisoning. Feedbacks among organisms and environments will ensure that both agencies are involved in extinction crises, and that both can radically alter species composition and patterns of interaction; but I shall argue on theoretical grounds and from available evidence that crises initiated by the elimination or addition of predators, competitors or pathogens will have a smaller reach and lead to less collateral extinction than crises initiated by conditions inimical to photosynthesis and leading to starvation.

The shrinkage or fragmentation of habitats is also commonly invoked as a major cause of extinction, especially in the modern era of deforestation and profound changes in land use and coastal modification. As I argue later, shrinkage and fragmentation make ecosystems more island-like and therefore render many environments too small to support certain species. However, shrinkage and fragmentation are not themselves agencies of extinction;

rather, they are outcomes of other, more fundamental causes, which today are overwhelmingly human in origin but which can also result from changing climate or geography brought about by novel physical and biological conditions.

DEMAND-SIDE EXTINCTION AND HABITAT REDUCTION

A change in the abundance and composition of key species is expected to initiate local to regional cascades that do not result in significant collateral extinction except under unusual circumstances. This is so for three reasons: (1) rarity of total exclusion of one species by another, except in island-like environments; (2) dependence of each species on many other species; and (3) redundancy of ecological roles, of substitutibility of species.

First, total exclusion of a species by another species – a competitor, predator or pathogen – is rare in nature. This is so because of three extremely widespread circumstances that permit co-existence between victims and enemies. These are: (1) adaptation, enabling individuals of the victim species to survive encounters with enemies often enough to leave offspring and to sustain the populations; (2) high fecundity, compensating for high rates of loss to enemy species; and (3) refuges, times and places where rivals do not penetrate or where they function ineffectively. Conversely, we can expect one species to eliminate another if the victim species is unable to acquire or defend resources in the presence of its rival, has a reproductive rate insufficient to make up for individuals that succumb to enemies, and overlaps completely with its lethal rival and has nowhere to hide. In addition, as noted by Simberloff (1986), very small populations make species vulnerable to extinction because the death of even one of a few individuals as a consequence of everyday events may reduce genetic variation necessary for gene-based adaptation, cause all surviving individuals to be of the same gender, or impair the social organization of some species. Circumstances under which these conditions of elimination are satisfied, therefore, define the conditions in which extinction of one species by interaction with another can occur. One of these conditions is the arrival of new, powerful enemies with which victim species had no previous co-existence. A species can cause extinction only if it kills or otherwise reproductively disables every individual of the victim species. In other words, victim individuals are not adapted to the intruder or to other powerful species with similar properties of competitive, consumptive or reproductive performance. Lack of adaptation is most likely when the difference between the newcomer's performance and that of the most powerful enemies with which the victim species normally interacts is large. This will be the case on islands and in such island-like environments as lakes and mountaintops.

As Darwin (1859) already knew, species with high per-capita and population-wide levels of competitive and reproductive performance evolve mainly in effectively large, productive ecosystems or regions such as large continental land masses and adjacent seas, where the rates and stakes of competition and consumption are high and where the power to acquire and defend resources is least constrained by low temperatures, low nutrient supplies and other factors limiting metabolism and activity (Vermeij, 1978, 1999, 2003). Examples of such powerful species include aggressive social insects, weedy plants, warm-blooded vertebrates, large-bodied plants and animals, and pathogens infecting dense populations of hosts among which horizontal transmission is the rule. Maximum body size of the largest herbivorous and predatory vertebrates, for example, increases as the area of the inhabited land mass increases (Bakker, 1980; Burness *et al.*, 2001). This relationship holds for both ectotherms and endotherms, but it is especially strong for rapidly metabolizing endotherms (warm-blooded mammals and birds). The reason is that large per-capita demand for resources is associated with small population size, all else being equal. On very small land masses, populations of large endotherms would be vulnerable to stochastic extinction because very few individuals with low reproductive rates would saturate the environment. Large body size on islands is possible, of course, as witnessed by giant tortoises on Aldabra and the Galápagos Islands, but it comes with the price of very low metabolic rates (McNab, 1994; Dudley, 2000; Burness *et al.*, 2001).

It is on islands and in small island-like habitats where the difference between the most powerful native species and the power of invaders is greatest. The combination of small habitat size, reduced potential for evolving large body size and other traits associated with high performance, and selection in a regime dominated by relatively low-energy enemies places island endemics at great risk of extinction when powerful competitors from larger land masses are introduced by humans to islands. Because large mammals, aggressive social insects, mainland trees and many other kinds of species with high performance typically cannot cross water barriers, probably because they cannot shut down their metabolism during the long crossing (Vermeij, in press a), islands are normally shielded from invasion of such species. Exchanges of species among large land masses or among larger bodies of water should less often result in the extinction of species because native species will often already be adapted to species with performance characteristics comparable to those of invaders (Vermeij, 1991).

The second reason for expecting minor collateral extinction when the agents of extinction are other species is that most species depend on more than one other species for food, shelter, pollination, dispersal or other goods and services. This means that, even if one key species should become extinct, survivors affected by the loss of that species should not themselves become collateral casualties unless there is no other species to replace the extinct key player. Collateral extinction will occur if the unique host of a parasite or other dependent species becomes extinct. Such extreme host specificity, however, is uncommon even among organisms where it has been thought to be widespread, such as herbivorous insects, animal-dispersed and animal-pollinated plants, and symbiotic mutualists (Fox and Morrow, 1981; Novotny *et al.*, 2002). Multiple dependencies therefore ensure that avalanches intense enough to cause collateral extinction are short and do not spread far.

Third, most critical functions in ecosystems – supplying, regenerating and consuming resources – are performed by many species or, in the case of prokaryotic microbes, by cosmopolitan species (DeAngelis, 1992; Scarff and Bradley, 2002). This redundancy, therefore, protects ecosystems from the collateral loss of species when invaders eliminate vulnerable victims. Even when competitive dominants and top consumers disappear, their loss will alter relationships and composition within communities, but will not cripple the ecosystems they occupied and helped to create. The cascade of extinction initiated by the invasion of powerful competitors will therefore be short and slow, leaving the recipient ecosystems changed but with most of their active species viable.

Reductions in effective ecosystem size similarly should trigger short extinction cascades. Most at risk are: (1) species with small populations and low fecundity that depend on large ecosystems; (2) species whose individuals range widely but whose breeding takes place in a small number of sites; and (3) species in which very few individuals in a few places supply most of the next generation's members. Large-bodied herbivorous and carnivorous mammals with large appetites, low birth rates (often less than one offspring per year) and low population density require large individual ranges (Kiltie, 1984; Kelt and Van Vuren, 2001). Habitat fragmentation or shrinkage would make these species inviable. Many marine mammals and seabirds breed in just a few places, even though individuals range extremely widely (Warheit and Lindberg, 1988; Vermeij, 1993b), making them susceptible to extinction through the loss of key sites. Many other species may also show this pattern of geographically restricted breeding. In others, perhaps including many marine invertebrates, reproduction may take place at many sites, but only a few scattered populations are large enough and dense enough to act as net sources of individuals, most other populations being sinks (see Holt, 1996; Holt and Gomulkiewicz, 1997; Jackson, 1995). We know too little about population structure to predict which, or how many, species are characterized by just a few source populations, but it is important to note that these populations are apt to be concentrated in the most productive parts of a species' geographic range (Holt, 1996).

Because many species that exercise strong top-down evolutionary and ecological control over the phenotypes and distribution of other species depend on large ecosystems, habitat shrinkage and fragmentation may preferentially eliminate the most powerful competitors and consumers (Vermeij, 1999). With their loss, top-down control shifts to less powerful, less productive species. The reduced demand from consumers would then lead to an ecological equivalent of an economic recession, in which supply temporarily exceeds demand; but a new dynamic balance is re-established in which productivity in the remnant habitats is lower than it was in the ecosystem before shrinkage or fragmentation. Despite this decline, an overall ecological collapse should not be expected, because the machinery of production, though altered and in the hands of different and less productive species, remains essentially intact. However, if fragmented or refugial populations are subjected to further change, they are likely to face extinction in their diminished, more island-like ecosystems (Didham *et al.*, 1998; Duffy, 2002, 2003).

Empirical evidence for extinctions triggered by the gain or loss of particular species is consistent with these expectations. Most evidence comes from human-caused introduction or elimination of species. The disappearance of mastodonts through human hunting at the end of the Pleistocene in Alaska changed the vegetation from a steppe grassland to a less productive moss tundra (Zimov *et al.*, 1995; Zazula *et al.*, 2003). The contemporaneous extinction of gomphotheres and other large forest mammals in Central America may have transformed a relatively open woodland to the more familiar closed forest, and potentially doomed tree species whose dispersal required ingestion and preparation of their hard seeds in the gut of mammals (Janzen and Martin, 1982). The introduction or horses and cattle in the sixteenth century, perhaps together with the persistence of less effective native mammalian dispersers, prevented the extinction of mammal-dependent trees (Janzen and Martin, 1982). No known extinctions are thus associated with these examples of human-caused elimination of top terrestrial predators and herbivores. In eastern North America, while most large mammals became extinct during the transition from the Pleistocene to the Holocene, only one tree (the spruce *Picea critchfieldii*) is known to have become extinct (Jackson and Weng, 1999).

The regional extinction of sea otters in most parts of the North Pacific during the nineteenth and early twentieth centuries led to sharp increases in populations of prey sea urchins, whose grazing transformed lush kelp forests into unproductive coralline-algal pavements (Estes and Palmisano, 1974; Estes *et al.*, 1989). Changes in climate coupled with overfishing in the Bering Sea have recently caused killer whales to prey on sea otters (Estes *et al.*, 1998). These events have led to widespread shifts affecting species as different as bald eagles, salmon and seaweeds. Heavy exploitation by humans of the California spiny lobster similarly resulted in decreases in kelp and increased abundance of sea urchins (Tegner and Dayton, 1977; Tegner, 1980). The decimation, or 'ecological extinction', of dugongs in the tropical Pacific, large predatory reef fish throughout the marine tropics, oysters in Chesapeake Bay, blue crabs in Georgia, green turtles in the Caribbean and cod in the North Atlantic, among other examples, caused irreversible alterations in the species composition and structure of most shallow-water and pelagic marine ecosystems (Jackson, 1997; Jackson *et al.*, 2001; Silliman and Bertness, 2002; Baum *et al.*, 2003; Myers and Worm, 2003; Pandolfi *et al.*, 2003; Worm and Myers, 2003).

The disappearance of the Atlantic grey whale after 1675 (Mead and Mitchell, 1984) must have transformed the seafloor of the North Sea and parts of the northwestern Atlantic from a heavily disturbed benthic community similar to that in the Pacific grey whale's feeding grounds in the Bering and Chukchi Seas to a community characterized by much shallower burrowing activity by animals. The extinction of the great auk, sea mink and Labrador duck in the coastal regions of the northeastern United States and eastern Canada must have reduced predation intensity on many invertebrates and fish, and therefore changed the selection regime of many species (see Vermeij, 1993b, 1996). Hundreds of species have invaded the eastern Mediterranean from the Red Sea through the Suez Canal, which opened in 1869. Remarkably, none of these cases is associated with collateral extinction of species (Vermeij, 1991; Carlton *et al.*, 1999).

It is very likely that some host-specific parasites were doomed when their hosts became extinct. Just such a single collateral extinction occurred when, in the early 1930s, a pathogen (quite possibly introduced) wiped out all populations of eelgrass from fully marine habitats in the northwestern Atlantic. The eelgrass limpet *Lottia alveus*, which lived and fed exclusively on eelgrass in full-strength seawater, became extinct at this time (Carlton *et al.*, 1991). Although eelgrass populations survived in brackish conditions and have since re-invaded high-salinity settings, the limpet lacked an estuarine refuge and therefore disappeared.

Readers will object that insufficient time has elapsed for species declines to result in extinction, and that many small or taxonomically poorly known species could have disappeared without our knowledge. It is in the nature of negative evidence that these possibilities cannot be ruled out. If recent extinctions were common, however, we would expect a high proportion of species known as Late Pleistocene fossils to be extinct. In a wide-ranging review of terrestrial species, Bennett (1997) showed that this is not the case. Deposits chronicling the last Late Pleistocene interglacial interval record many instances in which terrestrial and marine species occupied areas beyond the current range limits of these species, and it is clear that range limits have shifted repeatedly as climates changed (see also Lindberg and Lipps, 1996; Hewitt, 2000). Among marine molluscs, more than 90% of living species are known as Late Pleistocene fossils (Valentine, 1989). I know of just two Late Pleistocene marine molluscs that have subsequently become extinct: the northwestern Atlantic buccinid whelk *Atractodon stonei* (see Richards, 1962; Clarke *et al.*, 1972) and the Moroccan muricid dogwhelk *Spinucella plessisi* (see Vermeij, 1993a). Only two reef-building corals (out of about 60 species) in the Caribbean have become extinct, some time during the Pleistocene (Geister, 1977; Pandolfi *et al.*, 2002). Thus, despite the dramatic ecological changes wrought by the disappearance of top predators and herbivores in marine systems around the world (Jackson *et al.*, 2001), extinctions as recorded by fossilizable groups have been negligible until now.

Evidence indicates that collateral extinction resulting from the introduction or elimination of species has been important only on islands and in lakes. Extinctions since 1600 have eliminated a mean of 57% of bird species (range 0–100%) and a mean of 3.3% of plant species (range 0–14%) on islands (Sax *et al.*, 2002), as compared to less than 1% of bird species and plant species on continents (see also Diamond, 1984; Martin and Steadman, 1999). Human-introduced consumers – rats, cats, weasels, mongooses, snakes, snails and ants – wiped out small as well as large animals on islands, but their depredations were limited to their immediate victims and evidently did not extend to lower or higher trophic levels. In their analysis of extinction in New Zealand, Worthy and Holdaway (2002) identified only one plant species (a saprophytic mistletoe) as becoming extinct by the activities of a non-human agent, the Australian brush-tailed possum. In aquatic ecosystems, invasion-related extinction is demonstrable for endemic fish in many lakes, including Lake Lanao in the Philippines, Lake Poso in Sulawesi (Indonesia) and Lake Victoria in East Africa (Harrison and Stiassny, 1999).

Disturbances that reduce habitat size have driven many populations into decline and to local or regional extinction, but have not resulted in much collateral extinction of species. The positive relationships between habitat area and the number of species (summarized in MacArthur and Wilson, 1967) implies that species will become extinct as habitat shrinks, with a 20% loss of species for a halving of habitat area. In Singapore (540 km^2), a 95% reduction of forest cover over the last 183 years has caused local extinction among 5–7% of amphibians and reptiles, 25% of vascular plants and decapod crustaceans, and 34–43% of butterflies, birds, mammals and freshwater fish (Brook *et al.*, 2003). Further losses of now inviable populations may bring this level of local extinction closer to expectation as subsidy of Singapore's remnant populations from populations elsewhere diminishes. The monitoring of terrestrial islands artificially created in Panama and Venezuela when tracts of forest were submerged beneath rising waters of lakes shows that mainly large species, especially birds and mammals, were affected; spiders, lizards, ants, and small birds and mammals sometimes benefited from habitat fragmentation and contraction because of reduced predation and competition, and they replaced the larger animals as top consumers (Leigh *et al.*, 1993; Terborgh *et al.*, 2001). Among plants, fragmentation imperilled some large, insect-dependent trees, and favoured smaller, herbivore-resistant species that are more typical of disturbed or edge habitats (Leigh *et al.*, 1993; Terborgh *et al.*, 2001). Experimentally induced fragmentation in central Amazonian rainforest placed predatory beetles at higher risk of local extinction than beetles with other food habits (Didham *et al.*, 1998). Duffy (2003) showed that removal of individual consumer species, especially large-bodied vertebrates that suffer disproportionate extinction following habitat fragmentation, brought about larger decreases in plant biomass in terrestrial ecosystems than did the removal of individual plant species, which are less prone to extinction through habitat shrinkage.

Superficially, my contention that top-down dismantling of ecosystems and habitat shrinkage result in few extinctions and a low rate of extinction is at odds with the contention by May *et al.* (1995) that the rate of extinction today is high. May *et al.* (1995) estimated mean expected species lifespans by three independent methods related to changes in conservation status in official lists of threatened and extinct terrestrial species. Given the average rate of 0.8–2.0% habitat loss of tropical rainforest area per year, May *et al.* (1995) calculated that the average expected lifespan of forest species ranges from 300 to 1000 years, vastly shorter than the mean lifespan of fossil species (1–2 million years for mammals, 1–10 million years for marine species). The rate of extinction today is thus much higher than the rate of extinction observed during 'normal' times in the geological past. These rates, however, cannot be directly compared. The fossil record does not capture most endemic species and very few island species, the very taxa whose vulnerability to extinction today is highest. Moreover, the species now extinct or most threatened are those that, for demographic or other reasons, are the species most at risk of extinction to begin with. As these vulnerable species are lost, the rate of extinction for the surviving taxa should drop even under constant rates of habitat loss. Moreover, the vast majority of species that have become extinct and are threatened with extinction today are island species. Taking their risk of extinction and transferring that risk to continental (not to mention marine) settings is unwarranted, and leads to excessively high estimates of future extinction risk. Finally, May *et al.* (1995) did not consider the scope of collateral extinction, and implied instead that species become extinct independently of each other. If species become extinct in cohorts because their disappearances are causally linked, expected lifespans may be poor predictors of future or past risk.

In summary, on time scales of 10 years to 10,000 years, collateral extinction in continental and marine environments is very limited when key species are added or subtracted or when habitats fragment. Only on islands and in lakes (island-like freshwater habitats) does collateral extinction due to these factors appear to be important, but even here the avalanches do not extend far beyond the species most immediately affected. As human activity increasingly fragments the biosphere into small island-like enclaves, the potential for extinction resulting from the introduction or elimination of key species will increase. This effect will be enhanced as species ranges shift under climatic warming. Importantly, however, primary production – a role filled typically by many species – is not interrupted, even if productivity often declines and species composition may change dramatically. Collateral extinctions due to fragmentation and the gain or loss of species thus proceed from the top, but leave the supply side of the system viable.

SUPPLY-SIDE EXTINCTION AND COLLAPSE

If changes in demand trigger short cascades of collateral extinction, disruptions in supply have potentially disastrous consequences for many species, especially when agencies interfering with photosynthesis make sustainability of species that depend on primary producers impossible. Primary producers that fix carbon by photosynthesis occupy the thin layer of the biosphere that is exposed to sunlight. When a disturbance prevents sunlight from reaching the Earth's surface, induces a cut-off in the supply of essential raw materials or compromises the metabolic machinery of life, the sharp drop in the productive capacity of affected ecosystems not only kills many individuals and extinguishes many species outright, but in addition unleashes an avalanche of collateral extinctions.

The species most at risk of extinction are: (1) those without food or raw-material reserves; (2) those unable to protect their metabolic machinery from the elements or to shut down metabolism during at least one stage of the life cycle; and (3) animals such as herbivores, suspension-feeders and predators that directly or indirectly depend entirely on living primary producers for food or refuge. Less vulnerable species are those that consume dissolved organic matter, which persists in the sea for hundreds of thousands of years (del Giorgio and Duarte, 2002), and those that are supported by microbial primary producers using energy sources other than sunlight (Levinton, 1996; Jeffery, 2001). Organisms capable of suspended animation in a spore, cyst, egg, seed, tuber, bulb, or hibernating or aestivating adult are predisposed to cope with food deprivation and are therefore in a good position to weather photosynthesis-inhibiting disruptions.

Other essential ecosystem-level functions, such as the microbially mediated steps in the nitrogen cycle (Mancinelli, 2003), take place in a much larger segment of the biosphere, and are therefore less susceptible to disruption on regional to global spatial scales. Among the processes that sustain ecosystems, therefore, photosynthesis is the most vulnerable to disruption. Agencies interfering with photosynthesis are therefore most likely to trigger destructive outright extinction and far-reaching cascades of collateral species loss.

The mechanisms of supply-side extinction remain matters of vigorous debate and empirical research. To me, the most plausible mechanism leading to global crises in photosynthesis is darkness for periods lasting weeks to years. Clouds of smoke shielding the Earth's surface from the sun could form as droplets and minute particles are hurled into the atmosphere by collisions between Earth and objects from outer space, by huge volcanic flood-basalt eruptions, and by global fires initiated when lightning ignites methane released in vast quantities from anoxic ocean waters and sediments by the first two of these triggers (Ryskin, 2003; Vermeij, in press b). Olsen (1999) and MacLeod (2003) have noted that all the known mass extinctions of the last 250 million years are coincident with flood-basalt eruptions, although some evidence suggests that the Deccan Traps volcanism coinciding with the end-Cretaceous extinction actually began as much as half a million years before the crisis (Ravizza and Peucker-Ehrenbrink, 2003). Wignall (2001) and I (Vermeij, in press b) favour celestial impacts as the ultimate triggers for many of the extinction episodes. There is evidence for such impacts for the end-Permian, Late Triassic and end-Cretaceous extinctions (Wignall, 2001; Basu *et al.*, 2003). Even some smaller events could have been triggered by impacts of objects falling into the ocean, where diagnostic craters would not be obvious. Glikson (1999) and Norris *et al.* (2000), moreover, have given theoretical and empirical support to the hypothesis that impacts might trigger flood-basalt eruptions. Ivanov and Melosh (2003) have questioned this connection by noting that impact craters are not associated with local volcanism, but they do not address themselves to Glikson's (1999) hypothesis that shock waves from impacts trigger volcanism elsewhere at sites where magma is already welling up in the mantle. As discussed in detail by Ryskin (2003), methane dissolved in seawater or locked up in crystalline hydrate form in sediments could rise as gas bubbles from oxygen-poor waters and sediments and, in a period of weeks, enter the atmosphere in vast quantities (10^{18} to 10^{19} g). As the bubbles rise and expand, they carry with them anoxic water to the ocean surface, killing most oxygen-dependent life forms, including highly vulnerable phytoplankters and symbiont-bearing photosynthesizing animal protists. A flood surge associated with the catastrophic release of methane would inundate adjacent land with seawater and lightning could spark massive explosions and global fires, eliminating vast swaths of terrestrial vegetation (Ryskin, 2003).

In this scenario, extinction of the most vulnerable small primary producers in the sea and of combustible vegetation on land would take place over a very brief interval, from weeks to months, with the cascade of collateral extinctions taking a little longer after the initial catastrophe. These durations are substantially shorter than the time resolution available for even the most detailed sequences containing the sediments that chronicle extinction events.

Phenomena frequently observed to accompany mass extinctions are consistent with the methane-release scenario triggered by collisions or volcanism. Most notable are major disruptions in the carbon cycle, as indicated by sudden shifts in the carbon-isotopic ratios of fossil skeletons and sediments (for general discussions, see Brasier, 1995; Martin, 1995, 1998). These are known for all the Phanerozoic mass extinctions and for other less well known or smaller crises: the Late Neoproterozoic (Amthor *et al.*, 2003), Neoproterozoic–Cambrian transition (Hsu *et al.*, 1985; Gray *et al.*, 2003), end-Ordovician (Wang *et al.*, 1993), Late Devonian (Wang *et al.*, 1991; Racki, 1998), end-Permian (Wang *et al.*, 1994; Knoll *et al.*, 1996; Bowring *et al.*, 1998; Berner, 2002), end-Triassic (Pálfy *et al.*, 2001; Ward *et al.*, 2001), Early Jurassic (Hesselbo *et al.*, 2000), mid-Cretaceous (Paul and Mitchell, 1994; Leckie *et al.*, 2002), end-Cretaceous (Arthur *et al.*, 1987) and end-Paleocene (Bains *et al.*, 1999). These shifts are often accompanied by organisms or sediments indicating widespread anoxia in shallow waters (Brasier, 1995; Martin, 1995, 1998; Hallam and Wignall, 1997; Racki, 1998; Leckie *et al.*, 2002) and elimination of vertical stratification in ocean waters and pelagic ecosystems (Lipps, 1986; Knoll *et al.*, 1996; Leckie *et al.*, 2002).

However, these conditions may also be consequences rather than contributory causes of disruptions that interfere with primary production. The ecological expansion of species tolerant of oxygen-poor conditions from deep, oxygen-starved marine zones to shallow waters is often observed during extinction crises (Hallam and Wignall, 1997; Leckie *et al.*, 2002), and is often interpreted as evidence that oxygen-poor conditions themselves have spread into the photic zone where photosynthesis takes place, but it could equally well reflect an invasion of shallow waters by these organisms once the incumbents in shallow-water environments were wiped out. Similarly, the apparent elimination of stratification in ocean waters may not be the consequence of mixing between deep and surface layers in the ocean, but instead may reflect the opportunistic spread of surviving planktonic species from specific zones they occupied before the extinction into zones not previously inhabited by them and vacated by the species that became extinct.

An additional explanation for the coincidence of organic-rich sediments with extinction is also consistent with supply-related disruption. Sediments rich in organic matter are mineralogically dominated by clays (illite and smectite), which provide sufficient surface area for the sorption of dissolved organic carbon (Kennedy *et al.*, 2002). Clay-rich sediments derive from enhanced chemical weathering on land and are therefore associated with rapid run-off, which itself may reflect denudation of plant cover (Kennedy *et al.*, 2002). The coincidence of clayey, organic-rich ocean sediments with extinctions during the Cretaceous (Leckie *et al.*, 2002) may therefore indicate disturbance to primary production on land as well as in the ocean.

Several potential causes of extinction have been proposed by palaeoceanographers and marine biologists, but these causes would appear to affect some marine species but no terrestrial ones. For example, a deepening of the thermocline in the ocean would depress primary productivity by surface phytoplankton (Barber, 1988). The thermocline separates nutrient-deprived surface waters from deeper waters where nutrients falling as dead phytoplankters, zooplankters and faecal pellets accumulate. Deepening of the thermocline and warming of surface waters occur today on a regional scale off western South America during El Niño-Southern Oscillation events. The 20-fold decrease in surface productivity off Peru during the 1981–1983 El Niño caused mortality and reproductive failure among fish, seabirds and marine mammals in the central and eastern tropical Pacific (Barber, 1988). Associated shifts in winds brought drought to Indonesia and Panama and greater rainfall to western South America and other parts of the world. The effects took hold within weeks to months. Although no species is known to have become extinct as a result of this or other El Niño events (Vermeij, 1990), it is conceivable that a scaled-up version of the disruptions could threaten some species with extinction. If so, most of the species affected would likely live in the ocean rather than on land. Similarly, freshening (reduced salinity) in the surface waters of the North Pacific beginning 2.73 million years ago (Ma) during the Pliocene prevented replenishment of surface waters with nutrients from below, and therefore effectively decreased surface primary productivity in the North Pacific (Haug *et al.*, 1999). Although this freshening may be causally linked to the first substantial southward spread of glaciers in the northern hemisphere, and thus to a cooling climate in most of the world (Haug *et al.*, 1999), it is likely that any extinction wrought by this oceanographic change would affect marine species.

Other regional reductions in photosynthesis are caused by long-term droughts and shorter growing seasons. These climatic changes would, however, be regional rather than global. Extinctions would occur mainly because species displaced by changed circumstances were unable to sustain themselves in reachable refuges. This is presumably what happened when glaciers surged southward in Europe, trapping many species in a potentially inhospitable zone between the southern limit of glaciers and the Mediterranean Sea.

Some palaeontologists have argued that extinction arises from eutrophication, or nutrient enrichment, rather than from nutrient starvation as I advocate here. This argument, however, hinges on two questionable claims. First, the addition of nutrients to ecosystems overwhelms aggregate demand of oxygen-consuming organisms for food and oxygen and therefore leads to a depletion of oxygen and thus to mass mortality. This mechanism, however, requires that the added nutrients are incorporated first by primary producers, because it is the death of primary producers rather than the nutrient overload itself that leads to decay and to oxygen depletion where dead remains accumulate. The organic-rich sediments accumulating on the ocean floor at the inception of a crisis contain the remains of dead, not living, plankton. The high organic content of these sediments therefore records high rates of mortality, not necessarily high rates of primary production (Brongersma-Sanders, 1957). This is true even today beneath areas of upwelling, because mass plankton mortality from time to time rather than consistently high productivity accounts for episodes of organic-rich sedimentation. The second claim for oversupply of nutrients as a cause of species loss is predicated on the observation that the addition of nutrients is associated at small spatial scales and short time scales with reductions in local species numbers (Odum, 1969). Species disappear because they are excluded by a few competitive dominants. There are two objections to this interpretation. The first is that competitive exclusion is typically a local rather than a species-wide phenomenon, because most victim species do not completely overlap with dominant competitors and therefore often persist in refuges. The second and more interesting objection is that the short-term effects of nutrient enrichment have been documented in human-modified ecosystems in which nutrient enrichment is invariably accompanied by human over-exploitation of consumers. In experiments conducted at several North Atlantic intertidal sites, Worm *et al.* (2002) showed that the addition of nutrients results in competitive exclusion of slow-growing seaweeds by faster-growing species only when herbivores are also reduced or eliminated. In the presence of an undiminished complement of consumers, the added nutrients are effectively absorbed by resident species without the local elimination of competitively subordinate plants. Experiments in more wave-exposed intertidal settings in Oregon revealed that the addition of nutrients to tidepools either increased the abundance and species richness of seaweeds or had no effect (Nielsen, 2003), and that long-lived rather than ephemeral seaweeds profited most from the addition. At least locally, therefore, nutrient enrichment does not always lead to a decrease in diversity, and when it does lead to a decrease, the effect of eutrophication is most deleterious to diversity if ephemeral primary producers profit most and if consumer biomass is low.

Moreover, nutrient enrichment is often a consequence of human-caused deforestation, destruction of wetlands and other activities that both destroy primary production and release nutrients through enhanced soil erosion. For example, the addition of land-derived sediments and nutrients to coral reefs, which thrive in nutrient-poor and clear warm waters, gives fast-growing algae (and in the most extreme cases phytoplankton) a competitive edge over symbiont-bearing reef-builders such as corals (Birkeland, 1989; Allmon and Ross, 2001; McCulloch *et al.*, 2003); but without human exploitation of mangrove and terrestrial coastal forests, these nutrients would likely not spread to reefs, but be stored and used in these coastal ecosystems. Nutrient enrichment, therefore, threatens ecosystems when demand by consumers, or production in neighbouring source ecosystems, is already diminished. The nutrient enrichment is, in fact, itself a consequence of photosynthesis-inhibiting conditions in ecosystems that serve as the sources of nutrients and sediments.

To summarize these arguments, curtailment of photosynthesis interferes with the productive capacity of ecosystems, and places many species at risk of outright extinction. As a result of these direct bottom-up losses, many additional species become vulnerable to collateral extinction.

All of the mass extinctions (Hallam and Wignall, 1997) are marked by the regional to global extinction of primary producers, including very large populations of phytoplankters. Species losses among preservable phytoplankters are documented for the crises of the end-Ordovician (Colbath, 1986; Sheehan, 2001), Late Devonian (Racki, 1998), end-Permian (Knoll *et al.*, 1996; Bowring *et al.*, 1998) and end-Cretaceous (Thierstein, 1982; Kitchell *et al.*, 1986). Bottom-dwelling animals with photosynthesizing symbionts in their tissues – corals, fusulinacean foraminifers, large richthofeniid and other brachiopods, and several groups of bivalves – were more susceptible to extinction at the end of the Permian, Triassic and Cretaceous than related forms without such symbionts (Cowen, 1983; Rhodes and Thayer, 1991; Rosen, 2000). Major land-plant extinctions, presumably associated with reductions in the supply of living biomass available to consumers, are known for the end-Permian, end-Triassic and end-Cretaceous events (Saito and Kaiho, 1986; Retallack, 1995; Wing and Boucher, 1998; McElwain *et al.*, 1999; Beerling *et al.*, 2001; Looy *et al.*, 2001; Twitchett *et al.*, 2001; Wilf *et al.*, 2003). The end-Permian and end-Cretaceous crises witnessed the disappearance of all terrestrial herbivorous vertebrates weighing more than 30 kg (Bakker, 1980). With the exception of the end-Ordovician events, the Phanerozoic mass extinctions are known or thought to have coincided with impacts of celestial objects (Wignall, 2001; Berner, 2002).

Most of the minor extinction events chronicled by the pre-Late Pleistocene fossil record similarly witnessed the disappearance of planktonic primary producers and consumers, and therefore probably reflect regional to global perturbations in primary production that becomes available to larger consumers. Of the 29 ‘minor’ Phanerozoic events discussed by Hallam and Wignall (1997), only the regional end-Jurassic and deep-sea end-Paleocene events are not associated with obvious planktonic extinctions. Even for these events, however, a role for lowered productivity is likely, because these events, together with the dozens of others that stratigraphers use to define time units of a million years or less throughout the Phanerozoic, are based on the disappearance and appearance of short-lived, diagnostic, widespread planktonic taxa. Terrestrial as well as marine primary producers were affected by 'minor' extinctions during the Stephanian (latest Carboniferous, about 300 Ma) (Tappan and Loeblich, 1988; Labandeira and Phillips, 2002) and the events of the Late Eocene and Early Oligocene (36 to 32 Ma) (Tappan and Loeblich, 1988; Qian, 2002).

At least three Pliocene extinction events on land and in the sea beginning 3.6 Ma, and a fourth minor Early Pleistocene event at about 0.9 Ma, are the most recent episodes of species loss not attributable to hominids. Although the magnitude of species loss among planktonic species was relatively modest (maximally 19–20% of planktonic Foraminifera during the Middle and Late Pliocene) (Wei and Kennet, 1986; Chapman, 2000), evidence from suspension-feeding animals points to a temporary reduction in that portion of planktonic production that is consumed by benthic species in the North Atlantic, northeastern Pacific and south-temperate zone. There was selective extinction of large-bodied suspension-feeding species within several clades of turritellid and calyptraeoidean gastropods, balanomorph barnacles, and bivalves (venerids, ostreids, mytilids, pectinids and corbulids) (Vermeij, 1989; Allmon, 1992; Zullo, 1992; Roopnarine, 1996; Anderson, 2001). In Atlantic Central America, suspension-feeding molluscs declined in abundance relative to species with other adult modes of feeding (Todd *et al.*, 2002). In the tropical western Atlantic, seagrasses and symbiont-bearing corals suffered major losses (Budd and Johnson, 1999; Domning, 2001), implicating a regional reduction in benthic primary productivity as well. Areas of the Atlantic and northeastern Pacific affected by the extinctions witnessed a cessation or interruption in the accumulation of biogenic silica and phosphate, which are typically associated with high primary productivity (Vermeij, 1989; Haug *et al.*, 1999). A series of terrestrial extinctions during the Pliocene and Early Pleistocene eliminated large numbers of both large and small mammals in Europe and North America, as well as temperate trees in Europe (Webb, 1984; Rees *et al.*, 2001), again implying a role for reduced plant productivity.

Whether the marine and terrestrial events of the past 3.6 million years are contemporaneous and therefore triggered by the same events remains to be demonstrated. If they are, mechanisms interfering with photosynthesis must affect life on land as well as in the benthos and plankton of the ocean. This would cast doubt on many of the causes that have been proposed to explain the Pliocene and Early Pleistocene extinctions, including cessation of upwelling in the western Atlantic (Allmon, 1992; Allmon *et al.*, 1996), lowering sea levels during cold spells (Paulay, 1990), changes in ocean circulation resulting from the opening of the Bering Strait (5.5 to 5.4 Ma) (Gladenkov *et al.*, 2002) or the emergence of the Central American isthmus beginning 3.1 to 3.6 Ma (Cronin and Dowsett, 1996). These mechanisms apply chiefly to conditions in the ocean. Cooling (Stanley, 1986; Beu, 1990; Petuch, 1997) and increased seasonality (Hazel, 1971; Stanley, 1986) more plausibly affect ecosystems on land as well as in the sea, but they cannot easily be reconciled with observed susceptibility of large-bodied suspension-feeders to extinction, and would in any case typically enable species to contract, expand or shift their distributions. All these mechanisms may be symptoms of as yet unrecognized triggers, which possibly include celestial impacts documented at 3.3 and 2.15 Ma in the southern hemisphere (Gersonde *et al.*, 1997; Schultz *et al.*, 1998).

Cases in which anoxia-related extinction is not obviously tied to a disruption in photosynthesis are few, and apply mainly to biotas in deep basins cut off from general ocean circulation by sills at times of low sea level. The best documented example comes from the Japan Sea, where endemic deep-water molluscs became extinct during Pleistocene glacial intervals (Amano *et al.*, 1996). Deep-sea extinctions at the end of the Ordovician

(440 Ma) (Sheehan, 2001) and Paleocene (55 Ma) (Kennett and Stott, 1991) may similarly be linked to isolation and stagnation of epicontinental seas and some ocean basins, respectively.

IMPLICATIONS

Although the causes of extinction are numerous and interdependent, I argue that they fall into two broad categories, and that they define two types of extinction. Agencies that dismantle ecosystems through the introduction or elimination of key predators, competitors or pathogens, or that fragment habitats, tend to act on local to regional scales, and precipitate ecological changes that fall short of causing widespread collateral extinction. This category of extinctions encompasses most of the extinctions caused directly or indirectly by human action until now. In the second type, agencies attack ecosystems by interfering directly with photosynthesis or the pathways that supply energy and raw materials for photosynthesis. These agencies tend to operate on regional to global scales, and bring about ecological collapse involving the collateral extinction of many species that are deprived of food and habitat normally provided by primary producers. This type of extinction characterizes the vast majority of pre-Pleistocene crises recorded by fossils. The chief difference between these two types of extinction is that the key role of production is preserved during crises of the first type, even if productivity is often reduced and species composition of producers is altered; whereas during crises of the second type, primary producers are direct targets, and the all-important role that these organisms play in supporting the rest of the ecosystem is irreparably damaged. Using extinction as the criterion, we can therefore say that crises initiated at the consumer level are less devastating than those initiated among primary producers because loss of producer species often engenders additional extinctions, whereas changes in consumption rarely do.

Introductions of species by humans, exploitation of top predators and herbivores, and fragmentation of habitats have become large-scale, essentially global disturbances. Given that most of the world's environments have therefore become more island-like, with impenetrable barriers having been thrown up between suitable refuges, and perhaps with fewer refuges available to species in many places, it is to be expected that extinction avalanches triggered by the introduction or elimination of key species and by habitat fragmentation will become longer and more destructive in the large land masses and in the ocean, where collateral extinctions emanating from these disturbances have previously been few in number. Moreover, as functional redundancy in ecosystems declines, as it already has in many reef ecosystems (Hughes, 1994; Jackson, 1997), resistance to top-down triggers of extinction may decrease to the point where the avalanches unleashed by these triggers will imperil a large number of species. The northern and southern limits of range of north-temperate and south-temperate species, respectively, are shifting poleward as the climate warms (Parmesan and Yohe, 2003; Root *et al.*, 2003). With continuous habitats, these range shifts can be negotiated by many species without extinction; but in the insular setting in which most species find themselves today, climate-related shifts may eliminate some populations and even whole species.

Even at the globalized scale of human activity, the extinctions perpetrated directly or indirectly by human action do not find many persuasive parallels, and are therefore not well modelled by the extinctions of the geological past. This does not mean that the geological extinctions are irrelevant to our current predicament. Urbanization, pollution and the destruction of many of the world's most productive ecosystems interfere with primary production on regional to global scales, and the non-human triggers that unleashed crises in earlier epochs and eras are likely to do so again. Accordingly, protecting the productive capacity of the biosphere is the most effective general strategy to prevent runaway extinction.

On land and increasingly in the marine coastal zone, productive natural ecosystems are being replaced in part by even more productive but less diverse systems in which primary production is in the hands of human-farmed domesticated species. We do not know if this type of replacement or this type of preservation of primary production will offer protection against extinction avalanches that will accompany future human-caused or 'natural' disruptions to the supply side of the biosphere. The modelling of avalanches under different conditions of diversity, productivity, functional redundancy and agencies of disruption is urgently needed. Meanwhile, the lessons of geological history cannot be ignored. Production provides opportunity for consumers, including powerful ones like ourselves; tampering with it initiates destructive avalanches that imperil the survival of the species we value and depend on as well as of our own species.

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