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Causes and Consequences of Species Extinctions

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The five largest mass die-offs in which 50–95% of species were eliminated occurred during the Ordovician [490–443 million years ago (mya)], Devonian (417–354 mya), Permian (299–250 mya), Triassic (251–200 mya), and Cretaceous (146–64 mya) periods. Most recently, human actions especially over the past two centuries have precipitated a global extinction crisis or the "sixth great extinction wave" comparable to the previous five. Increasing human populations over the last 50,000 years or so have left measurable negative footprints on biodiversity.

GLOSSARY

Allee effects. These factors cause a reduction in the growth rate of small populations as they decline (e.g., via reduced survival or reproductive success).

coextinction. Extinction of one species triggers the loss of another species.

extinction debt. This refers to the extinction of species or populations long after habitat alteration.

extinction vortex. As populations decline, an insidious mutual reinforcement occurs among biotic and abiotic processes driving population size downward to extinction.

extirpation. This refers to extinction of a population rather than of an entire species.

invasive species. These are nonindigenous species introduced to areas outside of their natural range that have become established and have spread.

megafauna. This refers to large-bodied (>44 kg) animals, commonly (but not exclusively) used to refer to the large mammal biota of the Pleistocene.

minimum viable population. This is the number of individuals in a population required to have a specified probability of persistence over a given period of time.

1. INTRODUCTION

In the Americas, charismatic large-bodied animals (megafauna) such as saber-toothed cats (*Smilodon* spp.), mammoths (*Mammuthus* spp.), and giant ground sloths (*Megalonyx jeffersonii*) vanished following human arrival some 11,000–13,000 years ago. Similar losses occurred in Australia 45,000 years ago, and in many oceanic islands within a few hundred years of the arrival of humans. Classic examples of the loss of island endemics include the dodo (*Raphus cucullatus*) from Mauritius, moas (e.g., *Dinornis maximus*) from New Zealand, and elephantbirds (*Aepyornis maximus*) from Madagascar. Megafaunal collapse during the late Pleistocene can largely be traced to a variety of negative human impacts, such as overharvesting, biological invasions, and habitat transformation.

The rate and extent of human-mediated extinctions are debated, but there is general agreement that extinction rates have soared over the past few hundred years, largely as a result of accelerated habitat destruction following European colonialism and the subsequent global expansion of the human population during the twentieth century. Humans are implicated directly or indirectly in the 100- to 10,000-fold increase in the "natural" or "background" extinction rate that normally occurs as a consequence of gradual environmental change, newly established competitive

interactions (by evolution or invasion), and occasional chance calamities such as fire, storms, or disease. The current and future extinction rates are estimated using a variety of measures such as species–area models and changes in the World Conservation Union's (IUCN) threat categories over time. Based on the global assessment of all known species, some 31, 12, and 20% of known amphibian, bird, and mammal species, respectively (by far the best-studied of all animal groups), are currently listed by the IUCN as under threat.

Just how many species are being lost each year is also hotly debated. Various estimates range from a few thousand to more than 100,000 species being extinguished every year, most without ever having been scientifically described. The large uncertainty comes mainly through the application of various species–area relationships that vary substantially among communities and habitats. Despite substantial prediction error, it is nevertheless certain that human actions are causing the structure and function of natural systems to unravel. The past five great extinctions shared some important commonalities: (1) they caused a catastrophic loss of global biodiversity; (2) they unfolded rapidly (at least in the context of evolutionary and geological time); (3) taxonomically, their impact was not random (that is, whole groups of related species were lost while other related groups remained largely unaffected); and (4) the survivors were often not previously dominant evolutionary groups. All four of these features are relevant to the current biodiversity crisis. This sixth great extinction is likely to be most catastrophic in tropical regions given the high species diversity there (more than two-thirds of all species) and the large, expanding human populations that threaten most species there as well.

The major "systematic drivers" of modern species loss are changes in land use (habitat loss degradation and fragmentation), overexploitation, invasive species, disease, climate change (global warming) connected to increasing concentration of atmospheric carbon dioxide, and increases in nitrogen deposition. Mechanisms for prehistoric (caused by humans >200 years ago) extinctions are likely to have been similar: overhunting, introduced predators and diseases, and habitat destruction when early people first arrived in virgin landscapes.

2. EXTINCTION DRIVERS

Some events can instantly eliminate all individuals of a particular species, such as an asteroid strike, a massive volcanic eruption, or even a rapid loss of large areas of unique and critical habitat because of deforestation. But ultimately, any phenomena that can cause mortality rates to exceed reproductive replacement over a sustained period can cause a species to become extinct. Such forces may act independently or synergistically, and it may be difficult to identify a single cause of a particular species extinction event. For instance, habitat loss may cause some extinctions directly by removing all individuals, but it can also be indirectly responsible for an extinction by facilitating the establishment of an invasive species or disease agent, improving access to human hunters, or altering biophysical conditions. As a result, any process that causes a population to dwindle may ultimately predispose that population to extinction.

Evidence to date suggests that deforestation is currently, and is projected to continue to be, the prime direct and indirect cause of reported extirpations. For example, it is predicted that up to 21% of Southeast Asian forest species will be lost by 2100 because of past and ongoing deforestation. Similar projections exist for biotas in other regions.

Overexploitation is also an important driver of extinctions among vertebrates and tends to operate synergistically with other drivers such as habitat loss. For example, roads and trails created to allow logging operations to penetrate into virgin forests make previously remote areas more accessible to human hunters, who can, in turn, cause the decline and eventual extirpation of forest species. It is estimated that overexploitation is a major threat to at least one-third of threatened birds and amphibians, with wildlife currently extracted from tropical forests at approximately six times the sustainable rate. In other words, the quantity, and most likely the diversity, of human prey—both fisheries and "bush" (wild) meat—are rapidly diminishing.

Megafauna—those species weighing in the tens to hundreds of kilograms—are among the most vulnerable to overexploitation. In general, a species' generation time (interval from birth to reproductive age) is a function of body mass (allometry), so larger, longer-lived, and slower-reproducing animal populations are generally unable to compensate for high rates of harvesting. Because slow-breeding large animals, such as apes, carnivores (e.g., the lion, *Panthera leo*), and African elephants (*Loxodonta africana*), are particularly vulnerable to hunting, the potential for population recovery in these animals over short time scales is low. As an example supporting this generality, there is evidence that 12 large vertebrate species have been extirpated from Vietnam, primarily because of excessive hunting, within the past 40 years. The Steller's sea cow (*Hydrodamalis gigas*), an aquatic herbivorous mammal that inhabited the Asian coast of the Bering Sea, is the quintessential example of the rapid demise of a

species as a result of overexploitation. Discovered in 1741, it became extinct by 1768 because of overhunting by sailors, seal hunters, and fur traders. This species was hunted for food, its skin for making boats, and its subcutaneous fat for use in oil lamps.

The ecosystem and biological community changes precipitated by invasive species represent another leading cause of biodiversity loss. Of 170 extinct species for which causes have been identified reliably, invasive species contributed directly to the demise of 91 (54%). In particular, the rates of extinctions occurring on islands have been greatly elevated by the introduction of novel predators. Several ecological and life-history attributes of island species, such as their naturally constrained geographic range, small population sizes, and particular traits (e.g., lack of flight in birds or lack of thorns in plants) make island biotas vulnerable to predation from invading species. For example, the introduction of the brown tree snake (*Boiga irregularis*) shortly after World War II wreaked havoc on the biodiversity of the island of Guam in the South Pacific. In all likelihood, tree snakes were directly responsible for the loss of 12 of 18 native bird species, and they also reduced the populations of other vertebrates such as flying foxes (*Pteropus mariannus*), mainly because of the inability of the island's native species to recognize the novel predator as a threat. Despite an annual expenditure of US$44.6 million for the management of this problem, tree snakes on Guam are still not under control, largely because of their ability to penetrate artificial snake barriers such as fences.

The mosquito *Culex quinquefasciatus* was inadvertently introduced to Hawaii in 1826, and the disease-causing parasite (*Plasmodium relictum*) it carries arrived soon after. Since then, avian malaria (in conjunction with other threats) has been responsible for the decline and extinction of some 60 species of endemic forest birds on the Hawaiian Islands. Having evolved in the absence of the disease, Hawaiian bird species were generally unable to cope with the debilitating effects of the novel parasite. However, more than 100 years after the establishment of the disease, some native thrushes (*Myadestes* spp.) are now showing resistance to the disease. Sadly, many of the remaining species, especially forest birds in the family Drepanididae, are still vulnerable and are now restricted to altitudes where temperatures are below the thermal tolerance limits of the mosquito vector. Global warming is predicted to increase the altitudinal distribution of the mosquito, thus spelling doom for disease-susceptible birds as mosquito-free habitats disappear. The most feasible method of reducing transmission of malaria is to reduce or eliminate vector mosquito populations through chemical treatments and the elimination of larval habitats.

Perhaps one of the most infamous examples of an invasion catastrophe occurred in the world's largest freshwater lake—Lake Victoria in tropical East Africa. Celebrated for its amazing collection of over 600 endemic haplochromine (i.e., formerly of the genus *Haplochromis*) cichlid fishes (Family Cichlidae), the Lake Victoria cichlid community is perhaps one of the most rapid, extensive, and recent vertebrate radiations known. There is also a rich community of endemic noncichlid fish that inhabit the Lake. In addition to the threats posed to this unique biota by a rapid rise in fisheries exploitation, human density, deforestation, and agriculture during the past century, without doubt the most devastating effect was the introduction of the predatory Nile perch (*Lates niloticus*) in the 1950s. This voracious predator, which can grow to more than 2 m in length, was introduced from lakes Albert and Turkana (Uganda and Kenya, respectively) to compensate for depleting commercial fisheries in Lake Victoria. Although the Nile perch population remained relatively low for several decades after its introduction, an eventual population explosion in the 1980s caused the devastating direct or indirect extinction of 200–400 cichlid species endemic to the Lake as well as the extinction of several noncichlid fish species. Although many other threats likely contributed to the observed extinctions, including direct overexploitation and eutrophication from agriculture and deforestation leading to a change in the algal plankton community, there are few other contemporary examples of such a rapid and massive extinction event involving a single group of closely related species.

Human-mediated climate change represents a potentially disastrous sleeping giant in terms of future biodiversity losses. Climate warming can affect species in five principal ways: (1) alterations of species densities (including altered community composition and structure); (2) range shifts, either poleward or upward in elevation; (3) behavioral changes, such as the phenology (seasonal timing of life cycle events) of migration, breeding, and flowering; (4) changes in morphology, such as body size; and (5) reduction in genetic diversity that leads to inbreeding depression. A related threat for island and coastal biotas is the predicted loss of habitat via inundation by rising sea levels. Although large fluctuations in climate have occurred regularly throughout Earth's history, the implications of anthropogenic global warming for contemporary biodiversity are particularly pessimistic because of the rate of change and previous heavy modification of landscapes by humans. Good empirical evidence for some of these effects is rare, and speculations abound, but

there are already many local or regional examples and model-based predictions that support the view that rapid climate change, acting in concert with other drivers of species loss and habitat degradation, will be one of the most pressing conservation issues global biodiversity faces over the coming centuries.

One glimpse of a possible future crisis comes from the highland forests of Monterverde (Costa Rica), where 40% (20 of 50) of frog and toad species disappeared following synchronous population crashes in 1987, with most crashes linked to a rapid progressive warming and drying of the local climate. The locally endemic golden toad (*Bufo periglenes*) was one of the high-profile casualties in this area. It has been suggested that climate warming resulted in a retreat of the clouds and a drying of the mountain habitats, making amphibians more susceptible to fungal and parasite outbreaks. Indeed, the pathogenic chytrid fungus *Batrachochytrium dendrobatidis*, which grows on amphibian skin and increases mortality rates, has been implicated in the loss of harlequin frogs (*Atelopus* spp.) in Central and South America and reductions in other amphibian populations elsewhere. It is hypothesized that warm and dry conditions may stress amphibians and make them more vulnerable to the fungal infection.

Irrespective of the reason for a population's decline from a large to small population size, unusual (and often random and detrimental) events assume prominence at low abundances. For instance, although competition among individuals is reduced at low densities and can induce a population rebound, a countervailing phenomenon known as the "Allee effect" can act to draw populations toward extinction by (for instance) disrupting behavioral patterns that depend on numbers (e.g., herd defense against predators) or by genetic threats such as inbreeding depression. Small populations, dominated by chance events and Allee effects, are often considered to have dipped below their "minimum viable population" size. Thus, once a major population decline has occurred (from habitat loss, overexploitation, or in response to many other possible stressors), an "extinction vortex" of positive feedback loops can doom species to extinction, even if the original threats have been alleviated. Further, many species may take decades to perish following habitat degradation. Although some species may withstand the initial shock of land clearing, factors such as the lack of food resources, breeding sites, and dispersers may make populations unviable, and they eventually succumb to extinction. This phenomenon evokes the concept of "living-dead" species, or those "committed to extinction." The eventual loss of such species is referred to as the "extinction debt" caused by past habitat loss. For example, even if net deforestation rates can be reduced or even halted, the extinction debt of remnant and secondary forest patches will see the extinction of countless remaining species over this interval.

3. EXTINCTION VULNERABILITY

Certain life-history, behavioral, morphological, and physiological characteristics appear to make some species more susceptible than others to the extinction drivers described above. In general, large-sized species with a restricted distribution that demonstrate habitat specialization tend to be at greater risk of extinction from human agency than others within their respective taxa (e.g., Javan rhinoceros, *Rhinoceros sondaicus*), especially to processes such as rapid habitat loss.

Because of their high habitat specificity and/or low population densities, rare species may be more prone to extinction than common species. The size of a species' range is also a major determinant of its extinction proneness. Small ranges may make species more vulnerable to stochastic perturbations, even if local abundance is high; for example, proportionally more passerines (perching birds) with relatively small geographic ranges in the Americas are at risk of extinction than their more widely distributed counterparts. Such trends are worrisome because those species with shrinking ranges as a result of adverse human activities become particularly vulnerable to other drivers such as climate change. Habitat loss also reduces the patch sizes necessary for species requiring large home ranges, making them vulnerable to extinction from a loss of subpopulation connectedness, reduced dispersal capacity, and the ensuing lower population viability.

Larger-bodied vertebrates are considered to be more extinction-prone than smaller-bodied ones when the threatening process unfolds rapidly or intensely. Indeed, threatened mammals are an order of magnitude heavier than nonthreatened ones. A common explanation for this trend is that body size is inversely correlated with population size, making large-bodied animals less abundant and more vulnerable to chronic environmental perturbations (while being buffered against short-term environmental fluctuations). The extinction proneness of large-bodied animals to human activities is further enhanced because of other correlated traits, such as their requirement of large area, greater food intake, high habitat specificity, and lower reproductive rate.

Large species can also be more vulnerable to human persecution such as hunting, whereas smaller species are generally more vulnerable to habitat loss. It is important, however, to be cautious when constructing

generalized rules regarding the role of body size in the extinction process. Because they have a slower reproductive rate, larger parrots are more vulnerable to overexploitation than smaller finches, despite fewer numbers of the former being captured for the pet trade. However, some smaller species (e.g., white-eyes, *Zosterops* spp.) with small population sizes are also vulnerable to extinction because of heavy harvest rates for the pet trade, suggesting that only when the threatening processes are approximately equivalent will the larger of two species being compared demonstrate a higher risk of extinction. In addition to body size, other morphological characteristics affect extinction proneness. For instance, large investment in secondary sexual characteristics may render highly dimorphic species less adaptable in a changing environment or more attractive to specimen or pet-trade collectors.

When an environment is altered abruptly or systematically at a rate above normal background change, or beyond the capacity of adaptation via natural selection, specialist species with narrow ecological niches often bear the brunt of progressively unfavorable conditions such habitat loss and degradation. For instance, highly specialized forest-dependent taxa are acutely vulnerable to extinction following deforestation and forest fragmentation. Possible mechanisms include reductions in breeding and feeding sites, increased predation, elevated soil erosion and nutrient loss, dispersal limitation, enhanced edge effects, and other stressors. Conversely, non-forest-dependent species or those that prefer open habitats are often better able to persist in disturbed landscapes and may even be favored by having fewer competitors or expanded ranges following deforestation. It is important to be aware that in relatively stable systems, evolution engenders the speciation of taxa that occupy all available niches so both specialist and generalist species can coexist. As a result, the rapid pace of habitat and climate change renders specialization a modern "curse" in evolutionary terms.

Foraging specialization is one mechanism that can compromise a species' ability to persist in altered habitats. Many studies have shown that frugivorous and insectivorous birds are more extinction-prone than other avian feeding guilds, with the lack of year-round access to fruiting plants in fragmented forests being the culprit for the former. A number of hypotheses have been proposed to explain the disappearance of insectivorous birds from deforested or fragmented areas. First, deforestation may impoverish the insect fauna and reduce selected insectivore microhabitats (e.g., dead leaves). Second, insectivores may be poor dispersers and have near-ground nesting habits, the latter trait making them more vulnerable to nest predators penetrating smaller forest fragments. Absence of some insectivorous bird species from small fragments may not be related to food scarcity; rather, it may result from their poorer dispersal abilities. The ability to disperse in birds and insects depends on morphological characteristics such as wing loading, and physiological restrictions such as intolerance to sunlight when moving within the nonforested matrix landscape separating fragments. As a result, poor dispersal ability may make certain species vulnerable to extinction because they cannot readily supplement sink habitats (habitats in which populations cannot replace themselves), supporting otherwise unviable subpopulations, or colonize new areas. Because of poor dispersal ability, patchy distributions, and generally low population densities, the genetic diversity of species in fragmented landscapes may be difficult to maintain, with the resulting inbreeding depression further reducing population size toward extinction. However, clear and quantitative demonstrations of the role of life-history traits in the extinction process of biotas are still rare.

4. CONSEQUENCES OF EXTINCTIONS

The extinction of certain species such as large predators and pollinators may have more devastating ecological consequences than the extinction of others. Ironically, avian vulnerability to predation is often exacerbated when certain large predatory species become rarer in tropical communities. For example, although large cats such as jaguars (*Panthera onca*) do not prey on small birds directly, they exert a limiting force on smaller predators such as medium-sized and small mammals (mesopredators), which become more abundant with the former species' decline. The corollary is that abundant mesopredators inflict an above-average predation rate on the eggs and nestlings of small birds. Although this "mesopredator-release" hypothesis has been applied largely to mammals (e.g., Australian dingoes, *Canis lupus*, suppressing foxes and cats; coyotes in California controlling cat abundance), the loss of large predatory birds such as the harpy eagle (*Harpia harpyja*) may have similar ecosystem effects. Similar mesopredator release has been demonstrated for the first time in the marine environment, where the overexploitation of large pelagic sharks resulted in an increase in rays and skates that eventually suppressed commercially important scallop populations. Likewise, does the disappearance of a competitor result in the niche expansion and higher densities of subordinate species? This phenomenon has been observed between unrelated taxa—the extinction of insectivorous birds from scrub forests of West Indian islands correlated

with the subsequent higher biomass of competing *Anolis* lizards.

Conservation biologists have traditionally focused on the study of the independent declines, extirpations, or extinctions of individual species while paying relatively less attention to the possible cascading effects of species coextinctions (e.g., hosts and their parasites). However, it is likely that many coextinctions between interdependent taxa have occurred, but most have gone unnoticed in these relatively understudied systems. For example, an extinct feather louse (*Columbicola extinctus*) was discovered in 1937, 23 years after likely coextinction with its host passenger pigeon (*Ectopistes migratorius*). Ecological processes disrupted by extinction or species decline may also lead to cascading and catastrophic coextinctions. Frugivorous animals and fruiting plants on which they depend have a key interaction linking plant reproduction and dispersal with animal nutrition. Thus, the two interdependent taxa are placed in jeopardy by habitat degradation. Many trees produce large, lipid-rich fruits adapted for animal dispersal, so the demise of avian frugivores may have serious consequences for forest regeneration, even if the initial drivers of habitat loss and degradation are annulled.

Essential ecosystem functions provided by forest invertebrates are also highly susceptible when species are lost after habitat loss and degradation. Acting as keystone species in Southeast Asian rainforests, figs rely on tiny (1–2 mm) species-specific wasps for their pollination. Some fig wasps may have limited dispersal ability, suggesting that forest disturbance can reduce wasp densities and, by proxy, the figs that they pollinate. Similarly, dung beetles are essential components of ecosystem function because they contribute heavily to nutrient-recycling processes, seed dispersal, and the reduction of disease risk associated with dung accumulation. In Venezuela, heavier dung beetles were more extinction-prone than lighter species on artificially created forested islands, which predicts particularly dire ecosystem functional loss given the former group's greater capacity to dispose of dung.

Almost all flowering plants in tropical rainforests are pollinated by animals, and an estimated one-third of the human diet in tropical countries is derived from insect-pollinated plants. Therefore, a decline of forest-dwelling pollinators impedes plant reproduction not only in forests but also in neighboring agricultural areas visited by these species. Lowland coffee (*Coffea canephora*) is an important tropical cash crop, and it depends on bees for cross-pollination. A study in Costa Rica found that forest bees increased coffee yield by 20% in fields within 1 km of the forest edge. Between 2000 and 2003, the pollination services provided by forest bees were worth US$60,000 to a 1100-ha farm. A forest patch as small as 20 ha located near farms can increase coffee yield and thus bring large economic benefits to the farmers. Such findings illustrate the imperative of preserving native forests near agroforestry systems to facilitate the travel by forest-dependent pollinating insects.

5. CONCLUSIONS

Although extinctions are a normal part of evolution, human modifications to the planet in the last few centuries, and perhaps even millennia, have greatly accelerated the rate at which extinctions occur. Habitat loss remains the main driver of extinctions, but it may act synergistically with other drivers such as overharvesting and pollution, and, in the future, climate change. Large-bodied species, rare species, and habitat specialists are particularly prone to extinction as a result of rapid human modifications of the planet. Extinctions can disrupt vital ecological processes such as pollination and seed dispersal, leading to cascading losses, ecosystem collapse, and a higher extinction rate overall.

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