EXTINCTIONS, MODERN EXAMPLES OF

Gábor. L. Lövei
University of Aarhus

GLOSSARY

extinction Disappearance of the last living individual of a species. Extinction can be "local ∼," if it concerns a definite population or location; we speak of "∼ in the wild" when the only individuals alive of a species are in captivity; and of "global ∼" when no living individual remains of a species.

extinction cascade A chain of extinctions triggered by the extinction of a particular species on which many others depend. Species affected by other species directly (parasites that live only on that species) or indirectly (predators that rely heavily on the species for food) linked with the extinct species through ecological links. Most species support other species: a number of specialist herbivores can depend on a plant species for food, or many parasites are host-specific (can only parasitize one species). When these supporting species die out, the dependent species also become extinct. This can trigger a chain of extinctions, the "∼." For example, when the passenger pigeon died out, at least two feather lice parasites followed it into extinction. "Coextinction" occurs when more than one species dies out at the same time (this by definition must happen when the host of an obligate parasite dies out).

first-contact extinctions A wave of extinction of species native to a continent or island, following the first arrival of humans to that area.

living dead A term coined by the American tropical biologist, Daniel Janzen, denoting the last living individuals of a species destined to extinction. By definition, extinction happens when the last individual of a species dies. In reality, however, extinction of a species can be certain even earlier. Most species need both males and females to reproduce. If there are no fertile individuals of one sex, the species is doomed to extinction even if several individuals are still alive. Similarly, below a certain population size, a species cannot form a self-sustaining population, and its numbers dwindle. The decline may take many years but its course cannot be easily altered.

metapopulation A group of populations belonging to the same species that are connected via regular migration to each other's habitat patches. Many species exist as metapopulations and this is probably the original "natural state" for even more species.

proximate cause(s) of extinction The actual immediate agent(s) that cause(s) a species to become extinct.

pseudoextinction Extinction of local populations is sometimes erroneously termed as "pseudo-extinction." This is misleading because global extinction proceeds through the stepping-stones of extinctions of local populations. There is no fundamental distinction between the extinction of a local population and the extinction of a species other than the species becomes extinct when the last local population dies out.

recolonization The reappearance of a species in an area where it has earlier been present, then became extinct.

species life span The time between the first appearance of a species in the fossil record and its disappearance. This time span is typically in the range of millions of years.

ultimate cause of extinction Being rare (few in number) and of limited distribution are precursors to extinction. The causes leading to rarity are the ultimate causes of extinction.

NO SPECIES LIVES FOREVER, and extinction is the ultimate fate of all living species. The fossil record indicates that a recent extinction wave affecting terrestrial vertebrates was parallel with the arrival of modern humans to areas formerly uninhabited by them. These modern instances of extinction started at around 40,000 years ago. On continents, large mammals (especially those >50 kg body mass) were affected, while on islands, the impacts were mainly felt by birds. The causes of these extinctions are not well known but hunting, habitat alteration, and the introduction of nonnative species have caused extinctions. Our knowledge about extinctions is very incomplete, due to bias in research by taxonomy (vertebrate groups are better studied), geography (northern areas have received more attention), habitat (terrestrial habitats are better known than marine ones), biological reasons (certain groups do not fossilize), and methodological problems (methods of excavation and identification). Consequently, we can only crudely estimate the current rate of extinction. Even so it is evident that humans generated a new mass extinction, affecting all species in all habitats, and, by the time it has run its course, it will potentially surpass the previous five mass extinction events in the history of Earth. This article only deals with examples of extinction in the Quaternary period (from the final period of the last Ice Age, 10,000 years ago).

I. SPECIES LIFE SPANS

The life span of a species can vary widely but no species lives forever. Fossil records indicate that the average life span of an invertebrate species is about 11 million years (My), while mammal species live for about 1 My (Table I). As a consequence, species existing today form only a small fraction of species that have ever lived. If we assume that the average life span of a species is 5–10 My, and multicellular organisms have been on Earth for a period of 600 My, the plant and animal species currently living are not more than 1–2% of all those that have ever lived. For marine invertebrates, an estimated 95% of the species that had ever existed are extinct today. Extinction is thus the natural fate of all living species.

Extinction could happen at any time, and one can say that extinction is occurring continuously. Most of these extinctions are of local populations. For many species, a landscape contains several suitable habitat patches but not all patches are occupied at all times. Species constantly recolonize unoccupied patches and go extinct in others. The local populations in these patches form a kind of network called as a "metapopulation." There is constant migration among the habitat patches, some of them (source patches) producing surplus individuals that colonize other patches; others are not so productive (sink patches). When a metapopulation cannot produce enough individuals to compensate for mortality, the species will become regionally extinct. This will result in a range contraction as regular migration between metapopulations does not occur.

Species may become globally rare and subsequently go extinct at any time. The "background rate of extinction" is estimated to be in the magnitude of 1–10

TABLE I

Estimates of species' life spans, from origination to extinction

Group	Estimated life span (My)
Dinoflagellates	13
All invertebrates	11
Cenozoic bivalves	10
Diatoms	8
Planktonic foraminifera	7
Echinoderms	6
Marine invertebrates	5–10
Marine animals	4–5
Cenozoic mammals	1–2
Mammals	1
All fossil groups	0.5–5

From May *et al.* (1995).

species/yr through the geological periods. However, significant extinctions in Earth's history occurred in clusters. During the last 500 My, there were five such "mass extinctions," wiping out large proportions of the then-living species. The fossil record related to these has been intensively studied and hotly debated, but without producing an accepted interpretation about their causes. Extinctions, affecting a more restricted group of species have also occurred on a smaller scale. Within those groups the extinctions were significant.

The most recent of such events commenced during the Late Quaternary, about 100,000 years before present (yBP), and started to intensify about 40,000 yBP. Since then, several hundreds of land vertebrates, mostly large species (>50 kg body mass) have gone extinct on different continents and islands, at different times. This extinction wave has not yet ended.

II. EXAMPLES, POSTGLACIAL

A. North American Extinctions

In late glacial North America (called the Wisconsin glaciation period, ending about 10,000 yBP), 71% of mid-latitude mammal genera were lost, while in Alaska, the same loss was 56%. This is the opposite that would be expected from environmental conditions—we expect that if climate is the cause of these extinctions, more northerly species would be more severely affected. According to their trophic position, 71% of the herbivores, 67% of the bears, and 50% of the dogs and cats became extinct. Many of these have lived through cycles of glacial and interglacial periods, and extinction was not biased toward either older or newer genera. Environmental changes are therefore thought unlikely to have caused these extinctions. On the contrary—general conditions were at their worst during the period preceding the extinctions—20,000–18,000 yBP. Conditions for large mammals have improved afterward, notably between 18,000 and 7000 yBP, when most extinctions occurred.

The postglacial extinctions are generally connected to the appearance of humans in the regions affected. The North American continent has suffered numerous avian extinctions during the end of the last glacial: 19 genera of birds became extinct during this period. In spite of taxonomic problems, as well as scarce records (10 of these birds are only known from the single area of the Rancho La Brea tar pits in metropolitan Los Angeles, USA), we can generalize that most of these extinct birds were large to very large by avian standards, and the loss of most or all of them can be attributed to ecological dependency on large mammals that also went extinct during the same time. The largest group of these extinct birds were raptors: condors, eagles, accipitrid vultures, and caracaras. Extant hunting birds, including eagles, feed on carrion, as well as live prey that they themselves captured, so it is safe to assume the same way of life for these birds. The disappearance of large mammals must have resulted in a significant reduction of the available food base. As a consequence, many of them became extinct. A similar extinction cascade can be observed in the only remaining continent with diverse large ungulate fauna, Africa: where game becomes scarce or disappears, vultures and eagles also disappear. This points to the plausibility of the extinction cascade hypothesis. Two other birds, *Panandris* and *Pyelorhamphus*, related to the North American icterids (Icteridae) of today, are thought to have been in a commensalist association with large herbivores—the "cowbirds" of the Pleistocene—and followed their hosts into extinctions. In Africa, there are several further groups of songbirds associated with large mammals, such as oxpeckers and drongos. It is probable that a variety of commensalist relationships also existed in the New World, and these must have been lost with the disappearance of most large mammals in North America.

B. Australian Extinctions

Australia, until the end of the last glacial, had a fauna of monotremes and marsupials that was as diverse as the placental faunas of other continents. In contrast to those, however, the Australian fauna was rich at the species if not the genus level, and it was not subjected to any significant intercontinental faunal exchange. This led to a homogeneous fauna that seems to have been unable to withstand ecological stress. During the Late Pleistocene, many species went extinct. This loss was comparable, in numbers of species, to extinctions on other continents. For example, while there existed only 15 genera versus the 32 in North America, the number of extinct species is about 60 in Australia and 51 in North America. All 19 species of marsupials heavier than 100 kg, and 22 of the 38 species between 10 and 100 kg have become extinct. Three reptiles and the ostrich-sized *Genyornis newtoni* have met the same fate. A few of the extinct animals are depicted in Fig. 1. The largest reptile was the varanid lizard *Megalania prisca*, which, at 7 m length, was probably a top predator. Among the extinct monotremes were large

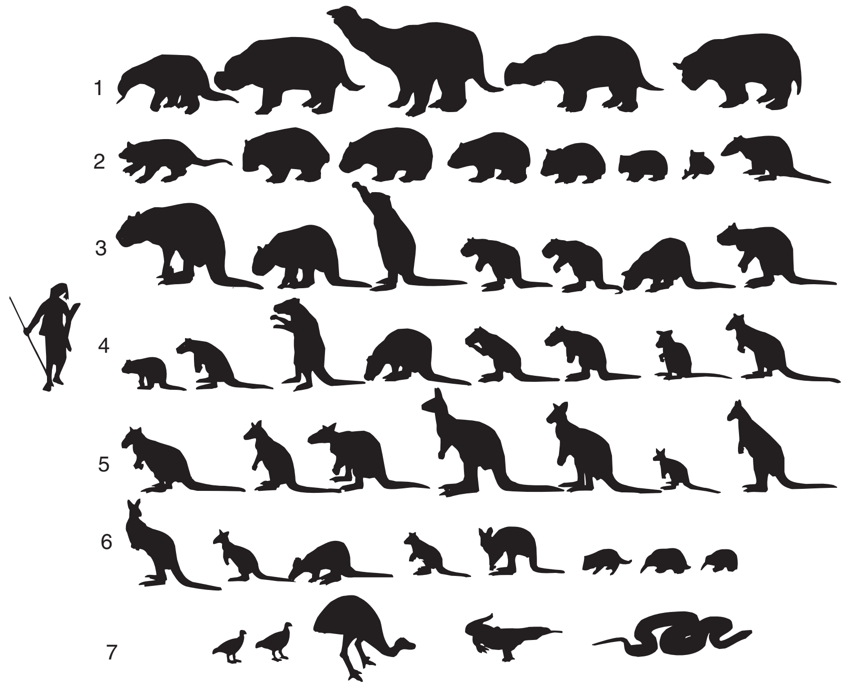

FIGURE 1 A bestiary of most extinct Late Pleistocene Australian vertebrate species. The silhouettes are drawn to scale, with the scale indicated by the human shape. The species, from left to right, are row 1: *Palorchestes azcal, Zygomaturus trilobus, Diprotodon optatum, D. minor, Euowenia grata*; row 2: *Thylacoleo carnifex, Ramsayia curvirostris, Phascolonus gigas, Phascolomys major, P. medius, Vombatus hacketti, Phascolarctos stirtoni, Propleopus oscillans*; row 3: *Proctoptodon goliah, P. rapha, P. pusio, Sthanturus maddocki, S. brownei, S. occidentalis, S. orientalis*; row 4: *S. gilli, S. atlas, S. tindalei, S. pales, S. oreas, S. andersoni, Troposodon minor, Wallabaia indra*; row 5: *Protemnodon roechus, P. anak, P. brehus, Macropus ferragus, M. birdselli, M. siva, M. titan*; row 6: *M. rama, M. thor, M. piltonensis, M. gouldi, M. stirtoni, Sarcophilus naliarius, Zaglossus hacketti, Z. ramsayi*; row 7: *Progura naracoortensis, P. gallinacea, Genyornis newtoni, Megalania prisca, Wonambi naracoortensis*. Reproduced with permission from Murray (1984). Copyright by University of Arizona Press, Tucson.

echidnas, such as *Zaglossus hacketti*, which was 1 m long and 0.5 m tall. This seems to have been a proportionately large version of the small living echidna. Among the marsupials, there were large carnivores: a large morph of the tiger cat (present on one island until European contact), or the leopard-sized *Thylacoleo carnifex*, a marsupial lion named "giant killer possum." One species of the koalas, *Phascolarctos sirtoni*, that was about 30% larger than the living koala, also survived until the very Late Pleistocene. The living koala is the only survivor of a diverse family that had its peak in the Tertiary.

The large and varied superfamily of Diprodontidea has totally disappeared during the Late Pleistocene, completing a longer sequence of decline. By the last glacial, only two families were represented. Some species of the Palorchestidae were beasts that resembled a giant kangaroo but had a tapir-like trunk and huge, curved claws. The cow-like *Zygomaturus trilobus* had a 2 m long body, a huge, broad head, and a narrow, upturned snout. Judging from the frequent fossil remains, it was widely distributed in coastal and mountain Australia. Another browser was the large, slow *Diprotodon optatum*, which had a feeding apparatus suggesting that it was browsing tough succulents and shrubs. The kangaroos (family Macropodidae) today are the largest group of marsupials still living in Australia, although their diversity, too, was seriously reduced by the beginning of the Holocene. From the *Macropus* genus itself, at least eight species died out. Some of these were small, like today's wallabies, but *Macropus titan* and *M. ferragus* were real giants, the latter reaching a height of more than 2.5 m and a body mass of 250 kg. If these species have a living relative, these are about 25% or smaller.

Although Australia has been inhabited by humans since at least 50,000 yBP, the extinctions were generally not believed to be linked to their presence.

Recent evidence based on more exact radiocarbon dating of bird and egg remains casts doubt on this belief, and human predation seems the probable cause also in Australian extinctions.

C. African Extinctions

When examples of modern extinctions are discussed, Africa is often ignored. Some have called Africa “the living Pleistocene” because this is the only continent where a diverse and abundant fauna remained that bears any resemblance to the Ice Age. However, Africa has had its postglacial extinctions and as this is the continent with the longest period of human occupation, the analysis of these is potentially very important.

The most impressive examples of such extinctions come from northern Africa. This region, after the dry, hyperarid period between 40,000 and 12,000 yBP, experienced a moist period during which the fauna included, among other species, the African elephant, white rhinoceros, zebra, warthog, giraffe, blue wildebeest, hartebeest, eland, roan antelope, and a species of reedbuck. Between 5000 and 4000 yBP, this moist period changed again, and this fauna disappeared from most of the Sahara, but survived in the Maghreb area of North Africa. Some species were certainly lost, though: the Atlantic gazelle (*Gazella atlantica*), Thomas’ camel (*Camelus thomasi*), the giant North African deer (*Megalocerus algericus*), and the long-horned North African buffalo (*Pelorovis antiquus*).

A similar cycle can be observed in southern Africa, although well-dated records are missing from most of this region. In the Cape zone, however, the total disappearance of the long-horned buffalo, giant hartebeest (*Megalotragus priscus*), the giant Cape horse (*Equus capensis*), and the southern springbok (*Antidorcas australis*) happened around 12,000–9500 yBP. Their extinction in southern Africa was, at least partially, related to climate-driven environmental change.

During this period, however, there was a dramatic change in artifact traditions throughout the continent, indicating a very significant shift in human cultures, and with this, probably of hunting techniques and efficiency. Analyses of archaeological sites support the hypothesis of increased hunting proficiency: more remains of individuals in their prime age were found, as well as relatively more bones of “dangerous game.” In North Africa, the appearance of domesticated animals may also have contributed to the decline.

The pace and extent of Late Pleistocene and Holocene extinctions in Africa parallel that of Eurasia, where there was no sudden and massive extinction wave such as in North America. The only significant difference between these continents and the Americas is the length of human occupation. After Africa, Eurasia has the longest period of human presence, about 700,000 years. North America did not have a previous history of human habitation, and the pattern of extinctions is entirely different. This continent was swept by waves of extinction during the Late Pleistocene/Early Holocene, coinciding with the migration through the Bering Strait and then southward of anatomically modern humans (Martin and Klein, 1984). During this period, a very large proportion of the extant fauna disappeared in what is geologically and evolutionarily a very short period of time.

III. EXAMPLES, FIRST-CONTACT EXTINCTIONS

On small islands all over the world, many species, especially birds, went extinct during the last 10,000 years (note that islands have an impoverished mammal fauna to start with, due to dispersal problems). The other common feature of these extinctions was that there was no taxonomic replacement of the lost species. These extinctions are so tightly correlated with the arrival of humans, that they were termed “first-contact extinctions” (FCEs). In the Americas, FCEs occurred between 12,000 and 10,500 yBP, in the West Indies 7000 and 5500 yBP, and in Madagascar 2000 and 500 yBP (MacPhee and Marx, 1997).

These FCEs can take as less as 1 year on small islands, and up to 1500 years on large islands and continents. On the Commander Islands, east of the Kamchatka Peninsula in the northern Pacific Ocean, humans arrived in 1741. Steller’s sea cow (*Hydrodamalis gigas*) was extinct by 1768. On the Mascarene Islands, humans arrived in AD 1600, and the major extinctions terminated around 1900. In New Zealand, the first human colonists arrived at around AD 1000, and the first major episode of extinctions terminated by AD 1500. In the Mediterranean, humans colonized all the major islands between 10,000 and 4000 yBP—this also coincides with the extinctions of several endemic species, such as pigmy elephants, rhinoceroses, and hippopotamuses.

A. Madagascar

The extinction of large mammals and birds on the island of Madagascar during the Holocene was of similar magnitude than the earlier, Quaternary extinctions in North America, Australia, and New Zealand. Today's Madagascar fauna is a pale shadow of a once-diverse assemblage of spectacular species, a "magnificent bestiary" (R. E. Dewar). Humans colonized Madagascar only in historical times. The earliest dated archaeological site is from about AD 500. The extinctions started to happen not much later. It is generally agreed that these extinctions were caused by human activities; opinion only differs in what type of activity this was.

Seven of the 17 primate genera have disappeared completely, and two more lost its largest species. The extinct lemuroids were all large, and probably diurnal. The largest of these, *Megadalapis edwardsi*, had males with a body mass between 50 and 100 kg. Members of the smallest extinct genus (*Mesopropithecus*) were about as large as the largest living species, the indri (*Indri indri*). Several of these species had ways of locomotion that are unknown among today's living primates: walking on the ground on four legs (*Hadropithecus*), arm-swinging (*Paleopropithecus*), and vertical climbing similar to that of the koala bear (*Megadalapis*).

The other group that was severely affected includes the large, flightless birds, ratites, commonly known as elephant birds. They are classified into two genera and 6–12 species. The largest of them (*Aepyornis maximus*) had a height of nearly 3 m, and resembled a massive ostrich. The smallest, *Mullerornis betsilei*, was about half this size. These species are thought to have been terrestrial grazers—this ecological group is otherwise only represented by the pigmy hippo (*Hippopotamus lemerlei*). This species, together with a large viverrid (*Cryptoprocta spelea*), and an endemic aardvark (*Plesiorycteropus madagascariensis*) is also extinct. *C. spelea* was the largest known carnivore in Madagascar, and resembled a short-legged puma—so much that earlier it was classified into the cat family (Felidae). The only reptiles that went extinct were giant land tortoises. The two species had carapace lengths of 80 and 120 cm, respectively, and were important consumers of ground vegetation.

B. The Pacific Islands

Humans have gradually colonized the world, and have reached several oceanic islands relatively recently. The colonization history of the Pacific Islands is relatively well studied. The human expansion across the Pacific, starting from SE Asia, was accompanied by a wave of bird extinctions on all the islands that humans reached. The time span of this varied due to facts such as distance from neighboring islands, area, and terrain—but the scale of the human-driven extinctions is huge. On all the Hawaiian Islands, we know more number of endemic species from fossil records alone than the number of such species now extant, that is, more than half the endemic species were lost after human arrival. Every island in Oceania had lost, on average, an estimated 10 species. The total number of islands is about 800, so the loss of species or populations totals to 8000. Rails have especially suffered. All Oceanic islands studied so far have had 1–4 endemic species of rails, and thus an estimated total of about 2000 species, equaling 25% of the global species richness, was lost during human colonization of the Pacific. Most of these species were flightless forest dwellers.

C. New Zealand

The New Zealand archipelago lies in the southern Pacific Ocean, between the latitudes of 30° and 47°. It is composed of two large and about 300 smaller islands. This land was originally part of the ancient supercontinent of Gondwanaland that also included Antarctica and the other Southern Hemisphere continents. New Zealand separated from Australia about 75 MyBP. To this day, its flora and fauna contains elements from this common landmass, from the time before it broke into separate continents. Because of its relatively large size and isolation, evolution took on a prosperous and original course, resulting in a high degree of endemism. New Zealand's fauna was characterized by birds and a few reptiles. Before the arrival of man, the only mammals were marine species and two small bats. There were no large predatory vertebrates, and in their absence, birds prospered. Many species arriving there with the power of flight had become unable to fly, but the best-known birds, the ratites, were originally flightless. The New Zealand ratites belong to two orders: the Apterygiformes (kiwis) and the Dinornithiformes (moas). They have probably been separated from their relatives since the Cretaceous. The kiwis remained small, unobtrusive, and nocturnal, and survived into the present.

Moas diversified into many species; current opinion accepts the existence of 12 of them. All were ostrich-like, flightless, herbivorous birds with a considerable size range. The largest moa, *Dinornis giganteus*, was about 2 m tall and weighed up to 250 kg, while the smallest, *Megalapteryx didinus,* was about the size of a large turkey, with an estimated live mass of 25 kg. In contrast to earlier opinion, it seems that most species inhabited forests, not grasslands. No species of the moas are left and this is one of the best-known examples of large-scale human-caused extinctions.

Polynesians successfully colonized New Zealand about 1000–800 yBP and although we neither have a reliable record of moa densities before or after this period, nor do we know about moa evolutionary history in earlier ages, it is well documented that the cause of their demise was that Maori intensively hunted all species. Archaeological sites with large amount of moa bones are found all over New Zealand, some covering many hectares. The most detailed research on them was conducted on the eastern side of the South Island, and these convincingly demonstrate that man was a voracious hunter of moas: their nests were robbed, and their carcasses were probably utilized in a wasteful way. Dogs and rats introduced by man have probably also played a role in the extermination of moas, especially the smaller species. Moa hunting became intensive about one century after the arrival of the Maori, coinciding with a rapid growth in their numbers. Within a few centuries, hunting and forest burning accelerated the decline; by about 400 yBP, moas became so scarce that they were no longer systematically hunted. Continued habitat destruction, sporadic hunting, and probably predation by feral dogs continued to destroy birds, and none were left by the time of European settlement.

The extinct bird species that have never been seen by Europeans include not only the moas, but about 20 other bird species. These were often flightless (79% of all extinct species), ground-nesting (89%), diurnal (96%), and larger than the closest surviving relative (71%). Fifteen of these were endemic to New Zealand, and five were very similar to living Australian relatives. Not less than four of the 15 were rails, thus echoing the extinction patterns of the Pacific Islands (see earlier). Other birds lost include a flightless goose (*Cnemiornis calcitrans*), a giant rail (*Aptornis otidiformis*), a swan (*Cygnus sumnerensis*), and several flying birds. A coextinction with the moas was the disappearance of the giant eagle, *Harpagornis moorei*, the largest known flying bird; it was probably preying on moa. After the extinction of its prey, or possibly even earlier, when the prey became rare, the predator died out.

IV. EXAMPLES, HISTORICAL EXTINCTIONS (1600–)

Since AD 1500, during the "modern era," extinctions were closely correlated with the European expansion, starting with the discovery of America in 1492. The time span of resulting extinctions differs by species and the area affected, but it gradually expanded to include all areas and habitats of the Earth.

A. New Zealand

During the European period of occupation in New Zealand (although "discovered" by the Dutch seafarer Abel Tasman in 1642, settlement by Europeans did not start until about 1840), at least five further bird species have become extinct. There is no doubt that the environmental changes brought by Europeans in about 200 years exceed those caused by the Polynesian occupants during the preceding centuries. This difference, however, is not due to intent but due to the difference in technology. The impact of the initial colonization in terms of extinctions is larger and more obvious because the Polynesians arrived to predator-free islands.

One of the recently exterminated species is the Stephen Island wren (*Xenicus lyallii*), the only known flightless songbird. Stephen Island is a small island in the Cook Straight, between the North and the South Islands of New Zealand. The first specimen of this bird was brought to the lightkeeper's house by his cat. Described as a species new to science, it was exterminated by the same cat within 1 year (1894). No person has ever seen a live specimen.

The catastrophic impact of predator invasion is exemplified by another New Zealand story, the rat invasion of Big South Cape Island. Big South Cape Island lies south of the South Island, and was known to harbor several endangered species when in 1964, ship rats (*Rattus rattus*) got on shore from a shipwreck. In 2 years' time, the rats reached very high densities, and four species of birds endemic to New Zealand, one native bat species (greater short-tailed bat, *Mysticina tuberculata robusta*), and numerous invertebrates became extinct. Other species were removed from the island, and thus, for example, the South Island saddleback (*Philesturnus carunculatus*), a thrush-sized bird, survived.

Many more species of birds, reptiles, amphibians, sea mammals, and invertebrates have also suffered reductions of their former range. Typically, they became extinct on the main islands, surviving only on offshore ones that were typically—but accidentally—free from introduced mammals. For example, the tuatara, *Sphenodon punctatus* (with its sister species *S. guentheri*), the only living relative of the dinosaurs, has been found in early archaeological sites on the main islands.

Today it only survives on a few offshore islands. It did not survive on any island where Polynesian rats (*Rattus exulans*) are present, but is common on rat-free islands. Another example of on-islands-only species is the little spotted kiwi (*Apteryx oweni*) that had only one self-sustaining population on Kapiti Island near Wellington, and the recently discovered, undescribed tusked weta (a relative of grasshoppers).

B. Hawaiian Islands

The Hawaiian Islands are a group of volcanic islands, in distant isolation from any other landmass, in the middle of the Pacific Ocean. They were reached by Polynesian settlers at around AD 500. These islands have had a very diverse and unique fauna and flora, and especially the vertebrates were seriously decimated. The best documented, again, are the bird extinctions. The extinct species include two species of flightless geese, flightless ibises, rails, a long-legged owl, a sea eagle, a number of species of honeycreepers, and at least one species of crow (now a second species, the Hawaiian Crow, is also extinct in the wild). Further, there is a group of species that have living populations on one island or another, but not on the one where they were found as subfossils.

The patterns of extinction are strikingly similar to those of New Zealand, except that there are no large numbers of songbird extinctions reported from New Zealand. Man-induced changes in Hawaii may have been more extreme, or New Zealand originally did not have many songbirds.

Significant paleozoological findings are accumulating and it is difficult to draw a reliable and comprehensive picture about the original fauna of the Hawaiian Islands as well as a proper assessment of the extent and nature of extinctions. However, what we know now indicates that the effect of man as exterminator, direct or indirect, of the fauna of this island archipelago is much more significant than earlier thought. Authorities claim that our previous knowledge of the prehuman Hawaiian fauna was so poor and extant species richness patterns are so pale remains of the original one that ecological and biogeographical studies using recently collected data are critically weakened.

The prehistorically extinct birds of the Hawaiian Islands include one species of petrel, at least 10, mostly flightless species of geese, three flightless ibises, eight of rails, three of long-legged owls, one accipiter, two large crows, one large meliphagid, and 15 species of Hawaiian honeycreepers (relatives of finches).

In the early 1980s, the existence of 82 endemic bird species were known from the Hawaiian Islands. Fifty-three of these became extinct prehistorically (before 1778 when Captain Cook discovered the islands). Area and elevation show significant positive correlation with the number of fossil and historically recorded bird species: small and/or low islands lost more species than large and/or high ones. On Molokai, the smallest of the five largest islands, with an area of 676 km^2 and 1515 m a.s.l., there are 21 fossil and nine historically known species. On Hawaii, the largest and highest (10,646 km^2, 4206 m a.s.l.), three fossil and 23 historic species are known—although more fossil species are expected after more excavations are done.

C. Extinction Paradoxes

Interestingly, current extinction rates seem to be lowest in areas with a long history of human habitation.

Plant extinction rates in areas with Mediterranean climate are low, ranging from 1% of all species in West Australia to 0.15% in the Mediterranean itself. Current threats to plants are one order of magnitude larger: 10.2–15.2% of species are considered threatened. The suspected cause of the current low extinction rate is a "recording error": many of these extinctions occurred in the "prebotanical age." Indeed, the current extinction rates are lowest where agricultural cultivation has been the longest, 8000–6000 yBP. This is consistent with the view that most vulnerable species will have been lost by the time botanical investigations started.

Similarly, the proportion of bird fauna extinct on the Pacific Islands is inversely proportional to the length of human habitation of these islands: 80% of Hawaii's bird fauna is recently extinct or endangered against 10% on Vaunatu. Hawaii has been inhabited for about 1500 years, and Vanuatu for 4000 years. Pimm and co-workers (in Lawton and May, 1995) argue that the sensitive species have been eliminated by the first colonists before record-keeping began, and thus we have no direct evidence of first-contact extinctions in the Pacific.

V. EXAMPLES, EXTINCTION CASCADES

A species' "ecological environment" almost always includes other organisms that are essential for its survival. Species are linked through trophic links—they eat each other. Other vital ecological links include pollination, dispersal of seeds, and providing habitat. For example, bees, birds, and bats pollinate flowers; birds and mammals disperse seeds; and trees provide nesting holes for birds. The extinction of a species can have reverberating consequences, affecting other species that are, directly (such as obligate parasites) or indirectly (such as shared predators), linked with the extinct species through such ecological links. Most species support other ones: a plant species can have a number of specialist herbivores that depend on it for food, or many parasites are host-specific (can only parasitize one species). When these supporting species die out, the dependent species also become extinct. This can trigger a chain of extinctions, termed an "extinction cascade."

With the death of the last passenger pigeon, a female named Martha, who died in the zoo in Cincinnati, USA, in 1914, at least two species of feather lice that were obligate parasites of this species, must also have perished, although there is no mention of this in any list of extinct species.

All moas, a group of 12 species of ratites of different sizes went extinct not long after Polynesians settled in New Zealand. The largest known raptor, the giant eagle (*Harpagornis moorei*) also followed them into extinction. As there are large middens with thousands of moa bones at several sites in New Zealand but these do not contain bones of the eagle, it is thought that the eagle was not a victim of persecution or hunting, but became extinct after its food base, the formerly very common moa, disappeared.

Likewise, several bird species that went extinct in North America at the end of the Last Ice Age are suspected to have died out in an extinction cascade.

VI. PROBLEMS IN OUR UNDERSTANDING OF EXTINCTIONS

We are aware that our knowledge of the actual extent of even recent extinctions is very fragmented and incomplete. There is, in other words, a huge difference between documented and real extinctions. This is due to a series of reasons. Some of these can be overcome with the development of science, but several of them result from the organisms' biology.

How many species are there? We do not know, even to an order of magnitude, how many species we share the Earth with. Current estimates of global species richness tend to converge to a range from 3 to 15 million species. This has an obvious consequence for the estimation of extinction rates: 1000 species is a different relative share of a global total of 3 versus 15 million.

Record keeping is insufficient/inadequate. The documentation of extinction is also uneven, both geographically (mostly from islands and the northern temperate region) and taxonomically (higher organisms are better reported).

Since 1600, only 485 animal and 584 plant species are listed as extinct (Table II). We strongly suspect that even among vertebrate groups, documented extinctions are serious underestimates. For example, on the Solomon Islands, where 164 bird species have been recorded, 12 have not been seen this century, but only one is listed as extinct. In Malaysia, a 4-year search for 266 freshwater fish species reported in the last century found only 122, yet few are recorded as extinct.

The current method of documenting extinct species is not, biologically, entirely valid. A species becomes "officially extinct" with the death of the last living individual. A species may be destined to extinction long before this happens. If mortality surpasses reproductive success, a species may get onto an "extinction trajectory"—numbers will continuously decrease without reversal, but it will take many years or decades until all individuals perish. Likewise, if there are no reproductively successful pairs remaining, the species has no hope of surviving, even though not all individuals are dead yet. These species are termed the "living dead."

Sometimes species can go through a "genetic bottleneck" when populations become so small that genetic variability practically disappears. One such example is the cheetah (*Acinonyx jubatus*), a fast-running predator in the cat family, which must have gone through such a population crisis some thousand years ago. Today all living cheetahs are, genetically, virtually identical. Another, the black robin (*Petroica traversi*), a small, endemic songbird on the Chatham Islands of New Zealand, had only one fertile female in the 1980s. In one of the success stories of conservation, this species was brought back from the brink of extinction—but genetic variability of the species is much reduced (although apparently without detrimental effects). Without human intervention, this species would have become extinct.

We also have to consider that so many species (for example, up to 40% of beetle species kept in the Natural History Museum collection, London, UK) are recorded from only one location that it is difficult to assess anything but local extinctions.

Uneven recording effort. Documented insect extinctions are 100 times lower than vertebrate extinctions. The difference is even greater if we consider that the number of insects is certainly much greater than we know today. Part of this is due to a large difference in the effort we devote to study these groups. There are

TABLE II

Species in major taxa that have become extinct since 1600 or are threatened with extinction

	Total number of species			% Extinct	% Threatened in 2004
	Described (thousands)	Extinct since 1600	Listed as threatened in 2004		
Animals, total	1400	485	3,565	0.03	0.3
Invertebrates, total	1190.2	256	1,992	0.02	0.17
Mollusks	70	191	974	0.3	1
Crustaceans	40	4	429	0.01	1
Insects	950	61	559	0.006	0.06
Others	130.2	n.a.	30	n.a.	0.02
Vertebrates	57.7	229	5,188	0.4	9
Fishes	28.5	176	800	0.62	3
Amphibians	5.7	2	1,770	0.004	31
Reptiles	8.2	23	304	0.03	4
Birds	9.9	116	1,213	1.2	12
Mammals	5.4	169	1,101	3.1	20
Plants, total	287.7	588	8,321	0.2	2.9
Mosses	15	n.a.	80	n.a.	0.5
Ferns and allies	13	n.a.	140	n.a.	1
Gymnosperms	0.98	2	305	0.3	31
Dicotyledons	199.4	120	7,025	0.06	4
Monocotyledons	59.3	462	771	0.9	1
Palms	2.8	4	925	0.1	33
Total, animals + plants	1545.6	584	15,503	0.2	1

Combined from May *et al*. (1995) and IUCN (2004).

100 times more vertebrate than invertebrate taxonomists, and 10 times more taxonomists of flowering than of nonflowering plants. This uneven attention given by humankind to different groups is also evident from the rate of describing new species. This is only 0.03–0.05% new species/yr for birds. In tropical areas, one out of every 100 plant specimens (1%) is new for science; for insects, fungi, and marine macrofauna, this can reach 20–80%.

Taxonomic and habitat bias. Our knowledge is also very biased by habitats and taxonomic relationships. We know much more about forests than seas, and while most of the mammal or bird species of the world are known, this cannot be said of other important and species-rich groups of organisms such as fungi, nematodes, or arthropods.

The great taxonomic bias in our records is well exemplified in the 61 extinct insect species: 33 of these are butterflies and moths. These groups do not constitute more than half of all insect species (they are more likely to be ∼25%); their prevalence merely reflects that butterflies are much better studied than other insect groups. It is perhaps realistic that 51 of these are island species but 42 of them are from Hawaii, which is certainly overrepresented. Similarly, of the 10 extinct continental species, nine are from North America. This indicates the distribution of researchers, not the real distribution of threatened or extinct species.

Geographical bias. Our knowledge is particularly scant in areas of the Earth with the highest biological diversity, the tropics. Any change is much better documented in the northern temperate regions where only a minority of the global biodiversity can be found.

The geographical bias and variability reported in the literature include patterns that are real, while others are imaginary. Sixty-one percent of all recorded animal extinctions are from islands—this is probably a real pattern. The numerical preponderance of the Pacific Islands is due to both their large numbers and recent human colonization. However, that two-thirds of recent animal extinctions are from North America and the Caribbean, and 20% is from Australia are certainly artifacts. All 45 plant extinctions in Africa include species from the Cape flora, and two-thirds of continental plant extinctions are from North America and Australia. The rarity of such records from South America, Asia, and other regions of Africa is surely also an artifact.

Methodological obstacles. Some of the above artifacts are historical and irreparable. Further inaccuracies result because much of the extinction information is gathered by paleozoology. We have never witnessed these extinctions, and only remains of the extinct organisms are found. There are special difficulties in studying and interpreting fossil or subfossil material. Just to mention one, the screens used for sieving soil when excavating animal bones have been, until recently, too coarse to retain bones of small bird species. As a natural consequence, our knowledge of the true extent of bird extinctions is grossly biased because there are many more small than large species of birds (just as in other groups of organisms).

Inherent, biological problems. Most of our fossils are from marine organisms, mostly because they often have calcareous body parts that fossilize well. Fossilization on dry land is different: some groups in some climatic regions (e.g., insects in tropical climates) simply do not fossilize.

Bird extinctions are better known than those of other organisms because their skeletons fossilize better and their taxonomy, generally, is well established. In contrast, the original vegetation of the Hawaiian Island lowlands is a matter of conjecture as it was largely destroyed before botanists arrived to collect there. Entomologists can only speculate what the effect of this deforestation could have been for the arthropods as very few insects are preserved under Pacific island conditions.

VII. THEORETICAL ASPECTS OF EXTINCTION

The first step in the extinction process for a species is to become rare. It is conceptually useful to distinguish between ultimate causes of extinction (what causes species to be rare and thus vulnerable to extinction in the first case) and proximate causes of extinction (what is the actual cause of extinction). The latter generally include demographic and environmental stochasticity (random, large fluctuations in density and environmental conditions), genetic deterioration and social dysfunction, although their respective importance is not well understood. Ultimate causes include hunting, habitat destruction, invasion by introduced species, and pollution.

There are two general tendencies that are relevant for the study of extinctions.

1. Species that are widespread tend to be abundant as well, but the causes of this positive correlation are not well understood. This also means that species most at risk from extinction (those that are sensitive to proximate causes) have small geographic ranges, because they will also be locally rare. This double jeopardy may be serious when populations and ranges are artificially reduced by ultimate causes of extinction.
2. The distribution of tropical species is generally more restricted than that of temperate species. Smaller ranges have been documented for tropical than temperate-region trees, mollusks, crustacea (crabs and relatives), fish, amphibians, reptiles, and mammals. A related trend is that average population densities of individual species increase from the equator toward the poles (proven for invertebrates, mammals, and birds). This fits with trend 1, and is also consistent with a decline in range sizes toward the tropics.

As a consequence, disproportionately more tropical than temperate species are threatened with extinction. Of the 1029 threatened bird species, 442 live in tropical forests, more than twice the number of species living in wetlands, the next most threatened habitat category.

Most (direct as well as circumstantial) evidence indicates that most of the recent extinctions were caused by humans. Climate change has been invoked in some cases but the evidence for this is not strong. The actual human impact can be due to overhunting, habitat destruction, and voluntary or accidental introduction of nonnative species (mostly predators: cats, dogs, rats, or browsing herbivores: pigs, goats, sheep). It was also suggested that humans have spread an extremely virulent pathogen, causing a "hyperdisease." In mollusks, birds, and mammals, that went extinct since 1600 and have a known cause, 23% was due to hunting, 36% due to habitat destruction, and 39% due to the introduction of exotic organisms. Once again, our knowledge is rather sketchy: in mammals that became extinct since 1600, only 30% have an established proximate cause of extinction.

Introductions as a threat to species. Introduced species have often been implicated in the extinction of native species. Many introduced species, however, have had no detectable effect on ones in their new environments. The massive spread of organisms by humans to other areas of the globe may increase local diversity, but will result in large losses in global biodiversity. To understand the danger that panmixing of the Earth's fauna and flora signify, let us consider a thought experiment in island biogeography. Species richness on an island is largely determined by its area: the larger the area, the more species the island contains. The same applies for continents. For example, mammal species richness is related to the size of the individual continents. The resulting correlation allows to extrapolate the global species richness. A supercontinent, with an area equal to the total dry land on Earth would support about 2000 mammal species. Currently, there are about 4200 mammal species. Therefore, geographical isolation allowed evolution to generate nearly twice the biodiversity that could otherwise, on the basis of habitat area alone, be expected. As today human-assisted invasion is becoming a more and more prevalent biogeographic phenomenon, the individual continents are more and more like one supercontinent. It is not surprising that more extinctions are predicted, with possibly catastrophic consequences for biodiversity.

Often there is more than one cause for extinctions. For example, the kokako (*Callaeas cinerea*), an endemic wattlebird in New Zealand became extinct in most of its former distribution range (and is on the brink of global extinction) due to a combination of factors. These include the contraction and fragmentation of its original forest habitat plus the effects of introduced predators, mainly the European stoat (*Mustela erminea*) and the Australian brushtail possum (*Trichosurus vulpecula*).

Insights from population dynamics. A further difficulty in understanding extinction is that the actual process is also very imperfectly documented. Only a few documented examples exist that link population decline to changes in species distributions. The stepping-stones to global extinction are local extinctions, so it is logical to assume that as a species becomes more restricted and rare, its distribution range will become fragmented and gradually smaller. The decline of the European fir tree (*Abies* sp.) was indeed accompanied by population range fragmentation. The skipper butterfly (*Hesperia comma*) in Britain has crashed during the twentieth century. This process left scattered and highly fragmented populations by the 1950s. The same happened with many bird species in New Zealand (the kokako, the kaka *Nestor meridionalis*, a large parrot or the weka *Gallirallus australis,* a flightless rail).

The sensitivity of fragmented populations is underlined by a trend seen in the success of reintroduction attempts: Seventy-six percent of 133 documented reintroductions into former "core" areas succeeded while only 48% of 54 translocations to periphery or beyond did so. However, not all species show similar range dynamics in the process of becoming rare. The Kirtland's warbler (*Dendroica kirtlandii*), a small insectivorous bird living in North American forests, withdrew into the historical center of its range during a recent 60% population collapse.

Special traits related to density. While population densities typically fluctuate widely, some species are naturally rare. The study of rarity holds promise to understand processes related to extinction, although only vague clues are available today. It would be important to know, for example, if naturally and anthropogenically rare species are equally sensitive to proximate causes of extinction.

In plants, locally rare and geographically restricted species have lower levels of self-incompatibility, and poorer dispersal abilities. Rare plants are overrepresented in certain families (Scrophulariaceae and Lamiaceae) and underrepresented in others (Rosaceae), at least in North America. This may indicate that there are some biological traits and adaptations that are shared by rare species.

Populations of large-bodied species fluctuate less than smaller-bodied taxa (although the measurement of population variability is not as easy as the concept suggests), yet body size is not a useful predictor of extinction risk. In birds, body size was not a useful predictor of rates of population increase or decrease in a global sample of threatened species from 12 families at various trophic levels.

One important but counter-intuitive fact is that trophic position has no consistent effect on extinction. It is difficult to detect a consistent tendency for more frequent extinction of species at higher trophic levels, fossil or extant. This is complicated by the difficulty in separating body size and trophic position (species at higher trophic levels are mostly large). Top predators, in other words, are not more prone to extinction than consumers at other levels.

It seems that large-bodied species are vulnerable to ultimate causes of extinction (hunting and habitat destruction) but less so to proximate causes (their populations fluctuate less).

Time factor. The above important determinants are thought to vary in ecological time, 10–1000 years. However, as no species lives forever, there may be processes that are operating in evolutionary time. If range and abundance are also species-specific characteristics, some species will be more extinction-prone (i.e., naturally rare and restricted in distribution) than others.

Among songbirds on West Indian islands, older taxa occur on fewer islands, have more restricted habitat distributions, and have reduced population densities. However, body size—abundance plots within tribes of birds have more positive relationships than expected in taxonomically ancient tribes, meaning that large-bodied species in old tribes are more common than small-bodied ones. This could be the product of differential extinctions of large-bodied rare species over time.

Bivalves and gastropods in Cretaceous fossils achieved characteristic range sizes early in their history, and this changed little thereafter. In this group, locally endemic species have much higher chances of extinction than species from more cosmopolitan genera.

VIII. THE PRESENT: A FULL-FLEDGED MASS EXTINCTION

There are very few documented cases of extinction of lower organisms. This is an inevitable consequence of our ignorance of the degree of biodiversity of those groups. Given this, it is not surprising that the current rate of extinction can only be roughly guessed. It is extremely probable that the rate of recent extinctions is several magnitudes higher than the "background extinction rates" and probably surpasses any similar mass extinction events in the Earth's history.

Given the above deficiencies, we can only estimate current rates of extinction. Among the comparatively well-studied birds and mammals, the documented extinctions in the twentieth century numbers to about 100 species. There are a total of 14,000 species of these classes, so the documented extinction rate in this century is about 1%. This translates to an expected average life span of a bird or mammal species of around 10,000 years. This is 100–1000 times shorter than the average life span calculated from the fossil record.

Three different methods for predicting impending extinction rates suggest future life spans of birds and mammals of 200–400 years if current trends continue. These impending extinction rates are at least 10,000 times higher than background rates in the fossil record.

All evidence suggests that a sixth mass extinction event in the history of Earth is underway. While the total effect cannot yet be guessed, we know that the sixth mass extinction will be unique in the Earth's history. It will be the first resulting not from environmental changes but the extraordinary population growth and the activities of one species. Our species now uses an estimated 25–50% of terrestrial net primary productivity. This is without precedent, and will make the coming extinction qualitatively different from all previous mass extinctions. We know enough to realize the gravity of the problem. We need a more elaborate understanding of the phenomenon, how it affects different groups and geographic locations, as our conservation actions will become more and more critical for the future of life on Earth.

See Also the Following Articles

EXTINCTION, CAUSES OF • EXTINCTION, RATES OF • MASS EXTINCTIONS, CONCEPT OF

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