REVIEW

Biodiversity losses and conservation responses in the Anthropocene

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Biodiversity is essential to human well-being, but people have been reducing biodiversity throughout human history. Loss of species and degradation of ecosystems are likely to further accelerate in the coming years. Our understanding of this crisis is now clear, and world leaders have pledged to avert it. Nonetheless, global goals to reduce the rate of biodiversity loss have mostly not been achieved. However, many examples of conservation success show that losses can be halted and even reversed. Building on these lessons to turn the tide of biodiversity loss will require bold and innovative action to transform historical relationships between human populations and nature.

xtinction has always been a feature of life on Earth, but the domination of global ecosystems by people has caused a sharp rise in the rate of extinctions to far above prehuman levels. Loss of biodiversity affects the functioning of natural ecosystems and threatens human well-being. In this Review, we place the current extinction crisis in the context of long-term impacts of humanity and assess current trends in biodiversity loss. We identify successes as well as failures in our response to this crisis and draw lessons on what is needed to turn the tide of biodiversity loss.

A brief history of human-caused extinction

The imprint of humanity on biodiversity reaches back 2 million years, when our ancestors in the genus *Homo* began to use the large-carnivore niche in Africa. This was associated with a two-thirds decline in other large carnivores, as species such as sabretooth cats and long-legged hyenas disappeared (1). Diversity of large herbivores also declined. For example, the 12 species of elephants and their relatives living in Africa around 3 million years ago were reduced to two (2). Similar disappearances began elsewhere as species of *Homo* spread beyond Africa (3), then accelerated in step with the global expansion of *H. sapiens* through the past 60,000 years (Fig. 1A).

Even before the dawn of the modern era of extinctions in 1500 CE, the wave of extinctions that followed our species around the world had large impacts on biodiversity. At least 140 genera

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of mammals, more than 10% of the global total, were lost over the 100,000 years to 1500 CE (table S1), a pace of extinction that far exceeds background rates estimated from the fossil record (4). Similarly, 23% of the world's turtle and tortoise species have disappeared over approximately the past 300,000 years (5). Prehistoric occupation of Pacific islands alone was associated with extinction of at least 1000 bird species, which is around 10% of all birds (6). In New Zealand, 36% (44 of the original 117) of land bird species have gone extinct since human settlement began 750 years ago, most of them in the prehistoric period between Polynesian and European arrival (Fig. 1B). Most prehistoric extinctions were of terrestrial animal species, but marine biodiversity also declined because of local extirpations and loss of abundance as human use of the oceans expanded (7).

Prehistoric extinctions are predominantly associated with human arrival rather than climate change (8) and are best explained by the impacts of hunting (9). Habitat modification and predation by alien species were additional factors in some places, especially islands. Throughout the Pacific and Indian Oceans, human-lit fires transformed island ecosystems with unprecedented speed (10); in New Zealand, anthropogenic fire saw the loss of over 40% of forest cover in the drier lowland regions within 10 to 70 years of human arrival (11). The main causes of recent extinctions and declines continue to be overexploitation and conversion of habitat, along with invasive species, disease, and urban development (12). Global climate change is already causing large disruptions to ecosystems (13) and is likely to grow in importance as a cause of extinction.

Estimates of the recent rate of extinction are limited by poor knowledge of most species. Our best information is for vertebrates: At least 363 vertebrate species have gone extinct since 1500 CE, according to the International Union for the Conservation of Nature (IUCN) Red List (14). The rate of extinction of vertebrates rose through the past two centuries as human populations industrialized and grew (Fig. 1C and fig. S1). Levels of current threat of extinction in those groups of plants

and invertebrates that have been systematically assessed cover a similar range to vertebrates (Fig. 1D), suggesting that vertebrates provide a useful yardstick for patterns of species decline and extinction among less well-studied organisms. Systematic monitoring of birds and mammals shows that global levels of threat are increasing by 1 to 2% per decade (Fig. 1D). This masks rates of population decline that are often far greater. For example, coastal wetlands are fast disappearing because of encroachment by people (15). Among 155 species of coastal waterbirds from east Asia, populations are declining at rates of 5 to 9% per year and as much as 26% for some species (16).

Comparison of trends in recent extinctions with current levels of threat suggests that the rate of extinction may be about to increase. Extrapolation of recent trends suggests that there will between 269 and 350 further extinctions of birds and mammals by 2100 (fig. S1). However, 1341 birds and mammals are currently classed as Critically Endangered or Endangered and are therefore likely to be extinct by 2100 if the processes causing their endangerment continue to operate; the fact that most (85%) of these species are currently decreasing suggests that is the case (details are provided in the supplementary materials). That is, our knowledge of current threats suggests that the rate of extinction could soon rise to at least five times higher than it has been in the recent past (Fig. 1C).

Species loss and ecosystem change

All species are connected to others through ecological interactions. Extinctions therefore reverberate through ecosystems, as do extirpations of local populations and declines in abundance, which are widespread even in species not close to extinction (17). Past extinctions and population declines were apparently concentrated on large-bodied vertebrates (9). Disappearance of these animals removed powerful consumers with strong effects on ecosystem composition and function, both on land and in the oceans (9, 18). More generally, species declines disrupt many interactions, with far-reaching consequences for ecosystems (19). For example, many woody plants produce large fruits and rely on large vertebrates for seed dispersal (20). Large seed size is positively correlated with wood density and hence high carbon-storage capacity. Loss of mutualistic partners can therefore lead to tropical forests dominated by fast-growing, smallseeded plants with lower carbon stores (20). Growth of reef-building corals depends partly on abundance of large herbivorous fish. In the Caribbean, overfishing of these keystone herbivores over the past thousand years caused shifts from coral to algal dominance of reef habitat (21). The stability and productivity of commercial fisheries are enhanced by diversity of both fished and unfished species. Large declines in diversity over the past two centuries correlate with lower catches, lack of resilience to exploitation, and higher incidence of collapse of stocks, along with degradation of other values such as quality of coastal and estuarine waters (22).

Global responses

Several international initiatives have attempted to coordinate action to halt or reverse biodiversity loss. The most important is the Convention on Biological Diversity (CBD; www.cbd.int), to which 196 nations are party. In 2002, world leaders pledged through the CBD "to achieve by 2010 a significant reduction of the current rate of biodiversity loss." The 2010 target was succeeded by the "Aichi Biodiversity targets" for 2011–2020, a more complex plan to reduce loss of species and natural habitats and safeguard ecosystem services, while also improving planning, financing, knowledge, and benefits from sustainable management of the natural world.

The 2010 target was not reached (23), and thus

far there has been too little progress on most of the Aichi targets for them to be met by 2020 (24–26). Most indicators of the global state of species and ecosystems show continuing deterioration, with little or no evidence of recent slowdown in rates of change (24). Indicators of the capacity of ecosystems to provide ecological services also show declines, despite increases in the benefits that human populations derive from them, suggesting that the natural capital on which human populations depend is being rapidly run down (25).

The continuing decline of global biodiversity is clear despite weaknesses in our ability to monitor progress against targets (27, 28). We lack good indicators for some of the Aichi targets, and available indicators often give somewhat inconsistent signals. For example, The Biodiversity Intactness Index, based on models of effects of land use on species abundances (29), suggests that all human land use to date has reduced the abundance of species by a global average of ~15%. In contrast, the Living Planet Index estimates an average 58% population decline in monitored vertebrates worldwide since 1970 (30). In response to such problems, work is under way on a consistent set of Essential Biodiversity Variables (EBVs; http://geobon.org) to capture spatial and temporal change at the levels of genetics, species abundances, species traits, community composition, and ecosystem structure and function (28). There is also much potential for improved use of existing ecological records, such as the International Long-Term Ecological Research Sites network (ILTERS; www.ilternet.edu). These networks have broad coverage (Fig. 2) and use shared protocols to record ecolog"[O]ur knowledge of current threats suggests that the rate of extinction could soon rise to at least five times higher than it has been in the recent past."

ical changes over long periods (31) but are currently underused in assessments of global change.

Causes of failure

Years CE

Why have we failed to stem the tide of biodiversity loss? We suggest four interrelated reasons.

First, responses to biodiversity decline are being more than offset by rising pressures, related ultimately to increasing human population size and per capita consumption. Between 1993 and 2009, the Human Footprint index, a measure of cumulative human impacts on land, increased by 9%, mostly because of conversion of habitat for agriculture (Fig. 2) (32), whereas the total area of forest landscapes unmodified by human use fell by 7.2% between 2000 and 2013 (33). The area of ocean fished at high intensity (that is, removing >30% of available primary productivity) has increased since 1950 (34). A recent leveling off in that trend may represent the limit of productivity of wild fisheries as well as improvements in fishery management (34, 35), but cumulative human impacts continue to increase across two-thirds of the world's oceans, mainly owing to intensifying effects of climate change (35).

Year assessed

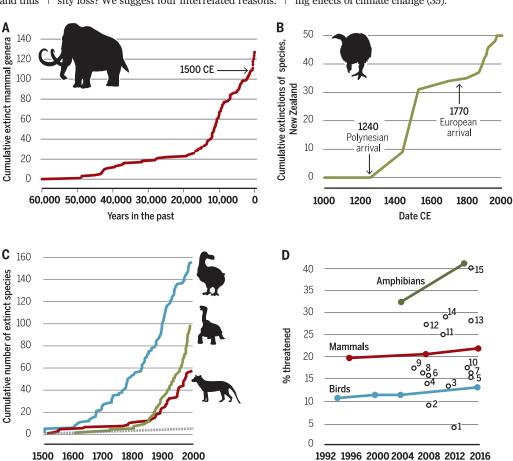


Fig. 1. Human-caused extinctions through time, and current levels of extinction risk. (A) Cumulative extinction of mammalian genera over the past 60,000 years. (B) Cumulative extinctions of vertebrate species in New Zealand over the past 1000 years. (C) Cumulative extinctions of vertebrate species worldwide since 1500 CE: birds (blue), mammals (red), and other vertebrates (green). Data are from the IUCN Red List (www.iucnredlist.org) and include listed species for which a date of last record or estimate of date of extinction is given in the species account. The gray line shows the number of species of mammals that should have gone extinct according to the background extinction rate estimated from the fossil record—two extinctions per million/species/years (68). (D) Recent trends in percent of species threatened in birds, mammals, and amphibians, compared with percent of species threatened in other groups of organisms that have been systematically assessed by using IUCN Red List criteria: 1, sea cucumbers; 2, Odonata; 3, reptiles; 4, seagrasses; 5, Bryophytes; 6, mangroves; 7, pteridophytes; 8, freshwater crabs; 9, sharks and rays; 10, freshwater shrimps; 11, freshwater crayfish; 12, reef-building corals; 13, cactuses; 14, freshwater fish; and 15, gymnosperms. Data sources are provided in the supplementary materials.

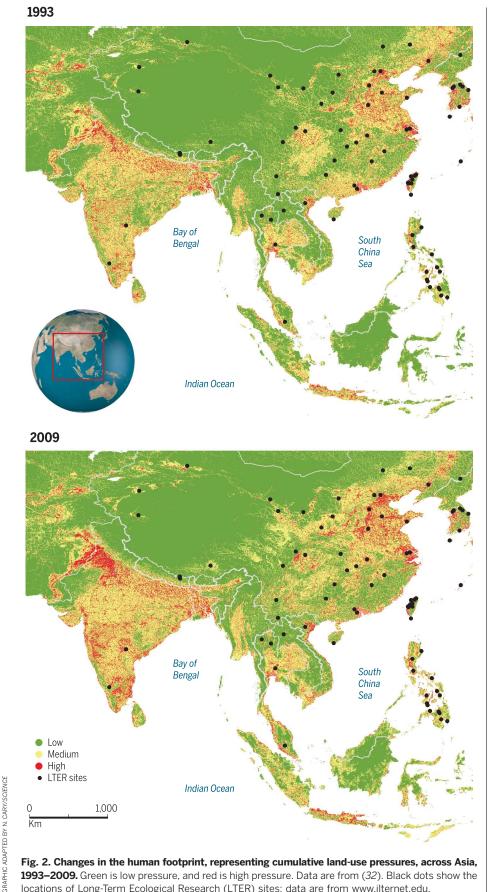


Fig. 2. Changes in the human footprint, representing cumulative land-use pressures, across Asia, 1993-2009. Green is low pressure, and red is high pressure. Data are from (32). Black dots show the locations of Long-Term Ecological Research (LTER) sites; data are from www.ilternet.edu.

Second, interactions and synergies among threatening processes often amplify their effects, producing large and accelerating combined impacts (36). Policy responses and actions tend to tackle threatening processes separately and are therefore often not appropriately scaled to pressures. A related problem is that some changes have large effects in catalyzing disparate threats (37). For example, road development in tropical forests has direct impacts by fragmenting habitat and causing mortality to wildlife but also triggers rapid escalation of a complex of threats, including overexploitation, conversion of marginal habitats for farming, fire, and invasive species (37-39). Climate change is likely to amplify impacts of other drivers of species decline; for example, there is evidence that rising temperature variability increases the susceptibility of amphibians to disease (40).

Third, funding for global conservation is inadequate. Total world spending on conservation for the period 2001-2008 was estimated at \$21.5 billion per vear (in 2005 U.S. dollars) (41). Most was domestic spending, of which 94% was in high-income countries. The developing world relies heavily on international aid for biodiversityconservation projects, but the sums available are typically insufficient for effective action (42). To make matters worse, threatened biodiversity is concentrated in those parts of the world where conservation is most underfunded (41). The Aichi targets include further mobilization of conservation finance, but evidence for recent increases in funding is equivocal at best (24).

Fourth, in most societies conservation is not mainstreamed into economic and social planning and human behavior (43). Conservation remains largely a discrete sector, which reacts as best it can to threats generated by other, more powerful sectors such as transport and agriculture. Conservation and sustainable use of ecosystems need to be embedded as primary societal concerns, like prevention of slavery and child labor. The marginalization of conservation means that fundamental drivers of biodiversity decline-such as rising per capita consumption, naïve economic models, and disconnection of people from natureare often ignored while the conservation sector does battle with their downstream effects. Analyses that include values of ecosystem services along with market values of products generated after habitat conversion demonstrate large net economic benefits from biodiversity conservation (44).

Effective conservation action

Amid the gloom, there are bright spots that show that conservation efforts can have impact. One of the brightest is the growth of protected areas, which should mean that the Aichi target of 17% coverage of the land surface by 2020 will be achieved (24, 26). Not all protected areas are effective, however, and evaluations give mixed results. Abundance of large land mammals in African protected areas declined by 59% between 1970 and 2005 (45), whereas a global synthesis concluded that wildlife populations are on average stable in terrestrial protected areas (46). Marine protected areas are most successful if they have effective enforcement of no-take policies and if the reserves are long-established, large, and isolated by deep water or sand (47). Future priorities are to use protected areas to maintain large contiguous natural areas with only limited human impact; to achieve representative coverage of habitats and species currently at high risk (48); and to secure key areas for provision of ecosystem services (49).

Conservation science is a mature discipline armed with knowledge and tools for effective management of populations and habitats. For example, analysis of the IUCN Red List showed that although the threat status of birds and mammals worsened over the two decades prior to 2008 (Fig. 1D), without recent conservation actions the situation would now be 18% worse still (Fig. 3, A and B) (50). In western Europe, the millennialong decline of large-bodied vertebrates has at last been turned around, as populations of large carnivores recover and large herbivores return to habitats from which they have been long absent. This is due to a combination of factors, including nature policy and legislation of the European Union, improved public attitudes, and rewilding of abandoned agricultural landscapes (51, 52).

These successes have come from management of high-priority species and landscapes. Tackling overexploitation and habitat loss over large regions is more difficult, but there have been successes. In waters of the United States and the northeast Atlantic, many large, highly managed fisheries have undergone reductions in fishing pressure and consequent increases in biomass since the 1990s (53). Attention is now turning to interventions such as catch shares and comanagement arrangements (54) to improve smaller, unassessed fisheries common in developing countries. More generally, community-based conservation (CBC) projects, which engage communities as stakeholders and devolve control over natural resources to them while improving access to benefits from sustainable use, show promise in reducing overexploitation and improving livelihoods (55).

Deforestation in the Brazilian Amazon has been reduced to around one-third of its peak in 2004, despite a recent spike (56). This was evidently due to many factors, including expansion of protected areas, improved enforcement of forestprotection codes and incentives for compliance with those codes, intensification of production of beef and soy on already cleared areas, and market embargoes against product from newly cleared lands (57). Production of soy and beef continued to grow as deforestation fell after 2005, and the retention of forest avoided the emission of 3.2 Gt of CO2 and should confer other benefits, including stabilization of river discharge and reduced risk of inhibition of rainfall, as well as retained biodiversity (57).

Efforts to sustain biodiversity in farmed landscapes have produced mixed results (58, 59). Conservation measures on farmland are often costly, and although some succeed, they typically reduce farm yields and hence are likely to displace production elsewhere (60). This has led instead to

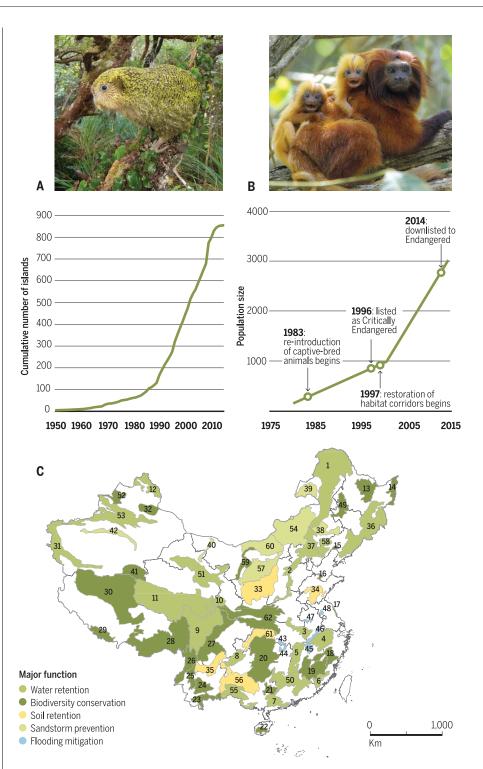


Fig. 3. Responses to biodiversity decline. (A) The cumulative number of islands on which one or more species of invasive vertebrates have been eradicated, since 1950. Data are from the Database of Island Invasive Species Eradications (http://diise.islandconservation.org). Island eradications of invasive predators have been essential in preventing the extinction of species such as the kakapo *Strigops habroptilus* (B) Recovery of the golden lion tamarin in Brazil. Reintroduction of captive-bred animals and restoration of corridors linking forest fragments have resulted in a dramatic increase in the wild population; shown are population estimates and intervention timeline from Associação Mico-Leão-Dourado. (C) China's National Ecosystem Function Zoning scheme, developed by the Ministry of Environment Protection and Chinese Academy of Sciences, to identify areas with key ecosystem functions and where development is restricted to protect those functions (source, www.mep.gov.cn/gkml/hbb/bgg/201511/t20151126_317777.htm).

calls for land-sparing: increasing yields on existing farmland in order to reduce pressure on remaining habitats and, in some instances, enable habitat restoration (60). If they are not simply to catalyze further agricultural expansion, land-sparing interventions need mechanisms that directly couple yield growth with habitat protection (61). Such initiatives would also be facilitated by explicit land-use zoning to distinguish areas where production is intensified and others to be spared.

One of our greatest immediate challenges is to minimize the impacts of new infrastructure development, especially in hotspots of biodiversity in the developing world. Large infrastructure projects are potentially damaging for two reasons. First, some projects have massive direct effects on entire ecosystems. For example, the Three Gorges Dam on the Yangtze River in China is disrupting the ecology of a region with 177 endemic fish species (62). Loss of top carnivores such as the Yangtze river dolphin Lipotes vexillifer and Chinese paddlefish Psephurus gladius is an early sign of ecosystem collapse (63), as is the decline in number of fish species recorded at Dongting Lake downstream of the dam, where species richness fell from 85 in 2003 to 66 in 2014, only 2 years after completion of the dam

Second, development of infrastructure frequently catalyzes many other threats and thereby triggers rapid escalation of total pressure on biodiversity. The scale of new developments is colossal. For example, 334 new hydropower dams are currently planned in the Amazon basin alone (65), and global road-building is likely to add 25 million km of paved roads by mid-century, almost all in developing countries (37). It is crucial that planning of these developments analyzes ecological effects as well as economic costs and benefits, to decide where infrastructure should be located to produce the most benefit for the least cost. For example, an analysis of roads currently planned for the 2.3 million km² Greater Mekong region of southeast Asia mapped areas where proposed developments are likely to furnish high gains in regional food production for low environmental impact, mainly by catalyzing higher productivity and market access in areas already converted for farming, and other new roads that would cause high impact for low gains in total yield (66).

The challenges identified above, of using spatial planning to optimize development versus conservation and adequately financing conservation, are being addressed in China through that country's ambitious Ecological Civilization plan (67). This includes prioritization of nationwide land use and infrastructure development based on a national zoning of ecosystem function (Fig. 3C) that is used to designate some areas as protected with restricted development and others with differing levels of development intensity. The strategy is being mainstreamed at all decision levels and implemented through mechanisms that include ecocompensation (of about 20 billion \$US per year) to areas where development is restricted and other tools including Green GDP (gross do-

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mestic product) auditing, carbon trading, pollutionrights trading, and property rights.

Conclusion

Although conservation efforts have produced some encouraging results, these have done little more than forestall some losses by tackling symptoms of unsustainable use of environments. Our successes have been valuable in buying time that could allow recovery of species and ecosystems in the future and providing lessons on how conservation actions can be made effective. However, the problem of transforming the fundamental drivers of unsustainable use of nature remains largely unaddressed.

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SUPPLEMENTARY MATERIALS

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