

Global Biodiversity Change: The Bad, the Good, and the Unknown

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Abstract

Global biodiversity change is one of the most pressing environmental issues of our time. Here, we review current scientific knowledge on global biodiversity change and identify the main knowledge gaps. We discuss two components of biodiversity change—biodiversity alterations and biodiversity loss—across four dimensions of biodiversity: species extinctions, species abundances, species distributions, and genetic diversity. We briefly review the impacts that modern humans and their ancestors have had on biodiversity and discuss the recent declines and alterations in biodiversity. We analyze the direct pressures on biodiversity change: habitat change, overexploitation, exotic species, pollution, and climate change. We discuss the underlying causes, such as demographic growth and resource use, and review existing scenario projections. We identify successes and impending opportunities in biodiversity policy and management, and highlight gaps in biodiversity monitoring and models. Finally, we discuss how the ecosystem services framework can be used to identify undesirable biodiversity change and allocate conservation efforts.

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1. INTRODUCTION

Biodiversity is the sum of all “plants, animals, fungi, and microorganisms on Earth, their

genotypic and phenotypic variation, and the communities and ecosystems of which they are a part” (1, p. 138), or simply stated, life on Earth (2). Biodiversity is multidimensional, and no single measure of biodiversity can capture all its dimensions (3). Biodiversity provides the foundation for ecosystem services, including nutrient cycling, climate regulation, food production, and the regulation of the water cycle, and it is therefore intimately linked with human well-being (2, 4, 5). This foundation is now becoming endangered as the human footprint on the planet increases and biodiversity declines. Species are becoming extinct at rates higher than in the fossil record of the past few million years, including the peak extinction rate owing to the megafauna disappearance at the end of the Pleistocene (6). Several other dimensions of biodiversity are also declining, such as the extent of tropical forests and the mean abundance of wild bird species (7, 8). The human appropriation of Earth’s natural resources is not only leading to biodiversity loss but also to large alterations of biodiversity distribution, composition, and abundance.

Here, we review our current understanding of global biodiversity change and its underlying drivers. We start by scoping our definition of global biodiversity change, which includes both biodiversity loss and biodiversity alterations. Next, we briefly review human-induced global biodiversity change since the last ice age to the Industrial Revolution. This provides a historical background for our discussion of recent biodiversity change, which is organized into four biodiversity dimensions: species extinctions, species abundances and community structure, species ranges, and genetic diversity. These dimensions are not by any means exhaustive but aim at being representative. We focus on terrestrial ecosystems, but we also give examples for freshwater and marine ecosystems. Next, we examine the direct drivers of biodiversity change: habitat change, overexploitation, pollution, biotic exchange, and climate change. Some of these drivers could also be considered dimensions of biodiversity, such as the change in quality of a habitat or biotic exchanges, but

for simplicity, we treat them only in the drivers section. We discuss how these drivers might evolve in the next few decades by reviewing existing social-ecological scenarios and the projections for indirect drivers, such as population growth, consumption patterns, and energy use. Although much of the news related to biodiversity change is worrying, we also provide an overview of future opportunities for reversing biodiversity declines and increasing biodiversity at the local level, as well as review some recent successes in biodiversity conservation. The next section discusses the gaps in our understanding of global biodiversity change, both in observations and modeling. We conclude with some thoughts on the nature of biodiversity change and the need to focus our management efforts on detrimental biodiversity change.

2. GLOBAL BIODIVERSITY CHANGE: ALTERATIONS AND LOSSES

Many organisms modify the environment and as a result increase their fitness or affect resource availability to other species, processes known as niche construction of ecosystem engineering (9). Humans and their hominid ancestors are no exception; they have been modifying ecosystems throughout history to improve food availability and decrease the success of their ecological competitors. What is truly exceptional about humans is the scale at which they have been able to modify ecosystems. The total industrial fixation of nitrogen (mainly for fertilizer production) together with biological fixation in crops, and nitrogen mobilized during fossil-fuel combustion, is greater than the nitrogen fixed by all natural processes together (10). Humans currently harvest about 15% of global terrestrial net primary production, using about six times more net primary production than was used by the extinct Pleistocene community of megaherbivores (11). More than 35–40% of the world's forests and other natural ice-free habitats have been converted to cropland and pasture (12, 13), a value that increases to about 70% in some

biomes, such as Mediterranean forests (2). Over half of the world's large river systems have been affected by dams (14), and 40% of the ocean is strongly affected by multiple drivers (15). Some of these impacts do not target specific species, such as altering the nitrogen cycle or land-use change, but may favor some functional groups. Other actions are directed at specific species or at least aim directly at some functional groups, such as hunting, fishing, and timber logging.

An important distinction should be made between biodiversity loss and biodiversity alterations (**Figure 1**). This issue is particularly important as it implies that not all biodiversity change is inherently a bad thing, and therefore we often need to define a set of criteria to assess the benefits and disadvantages of biodiversity change. Recent global species extinctions correspond to net biodiversity loss, as the number of species created by evolutionary processes occurs at a much slower pace than the recent extinction rates (6, 16). The loss of genetic diversity, particularly the disappearance of populations and particular alleles, also corresponds to biodiversity loss, although small alterations of genetic diversity may not correspond to significant biodiversity loss.

Much of human action alters the species composition and the relative species abundances in an ecosystem, changing the structure

Biodiversity: the sum of all organisms on Earth, their variation, and the ecosystems of which they are a part

Biodiversity loss: the local or global extinction of an allele or species

Drivers: direct or indirect pressures on biodiversity that induce a change (either negative or positive)

Biodiversity alterations: human-induced changes that lead to modifications of community structure or to shifts in species distributions

Scenarios: plausible stories about how the future may unfold, often associated with quantitative projections

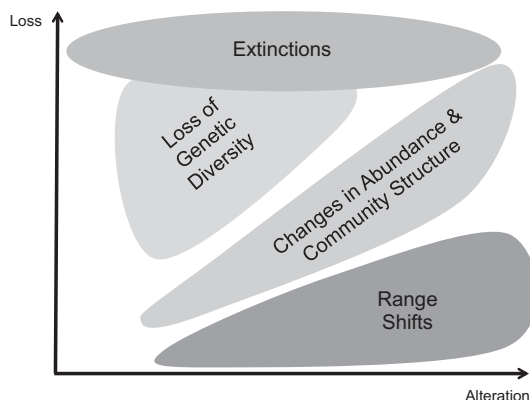


Figure 1

Conceptual diagram illustrating the intensity of loss and alterations associated with the different dimensions of biodiversity change: extinctions, loss of genetic diversity, changes in abundance and community structure, and range shifts.

of communities, but may not lead to biodiversity loss at the regional or global scale (**Figure 1**). For instance, the conversion of farmland into forest may lead to the decline of farmland bird populations but result in a population increase of forest species (17, 18). Still, large alterations in abundance and trophic structure may cause net biodiversity loss (**Figure 1**). For instance, the depletion of fisheries (19) or the overall decrease in the Living Planet Index (20) can certainly be considered net biodiversity loss.

Many shifts in species' range induced by climate or abiotic factors may not lead to a net biodiversity loss at the global scale (**Figure 1**). However, a local scale analysis can produce a very different result. Shifts in species distributions occur when a species goes locally extinct in some parts of its former range and colonizes new sites. Therefore, in a place where the species goes extinct, one can consider that biodiversity has been lost, while in a place that a species has colonized, one can consider that biodiversity has been gained. This last interpretation is however context dependent: The expansion of exotic species leads to an overall homogenization of global biodiversity that is arguably making the biosphere more monotonous and can threaten native species. The rearrangement of communities may also lead to the development of new communities, particularly for regions where new climates without current analogs develop (21).

3. A BRIEF HISTORICAL PERSPECTIVE ON GLOBAL BIODIVERSITY CHANGE: FROM THE ICE AGE TO THE INDUSTRIAL REVOLUTION

We can hypothesize that the first actions of humans with large-scale impacts on biodiversity were fire and hunting. It is difficult to date precisely when humans started controlling and manipulating fires. There have always been natural fires associated with lightning and volcanic activity, and therefore the co-occurrence in an archeological site of burning and artifacts does

not necessarily imply a causal link between the two (22, 23). The first intentional uses of fire were likely domestic, including cooking, heating, predator defense, illumination, and artifact manufacture and may have started as long as 1.9 Mya ago, although its widespread use seems to date back only to the beginning of the Middle Paleolithic, around 400,000–200,000 years ago or even later (**Figure 2**) (23–25). However, the systematic use of fire as an ecosystem management tool is perhaps much more recent, beginning tens of thousands of years ago (24). Landscape burning has several purposes, which include driving game into hunting areas, clearing thick vegetation for travel, and opening up grazing areas for game species (26). We know that some recent hunter-gatherer societies, such as Native America tribes and Australian Aborigines, managed landscapes with fire and that fire also played an important role in early agrarian and herding societies to maintain open vegetation and fertilize soil (26). Identifying how early landscape management by fire became a tool in hominids is harder, and a recent study has not found a significant difference in fire regime between the Neanderthal occupation and the arrival of modern humans in Europe (26). Evidence for change in fire regime in Southeast Asia and Australia goes back to about 40,000 years ago, but the Australia evidence has faced some recent challenges (26).

Hunting is likely to have driven the first wave of species extinctions induced by humans starting 50,000 years BP (**Figure 2**) (22, 27). The extinction of large-bodied vertebrates (i.e., megafauna; >44 kg) closely followed the global spread of *Homo sapiens* to new continents and islands. In Australia, 88% of the megafauna mammal genera went extinct between the time of human arrival, \approx 50,000 years BP, and 32,000 years BP (28). In North America, 72% of the megafauna mammal genera went extinct, mostly between 13,500 and 11,500 years BP (28), and shortly after the arrival of humans in the continent between 15,000 years BP (29, 30) and 13,000 years BP (31). In South America, 82% of the genera went extinct sometime between 12,000 and 8,000 years BP

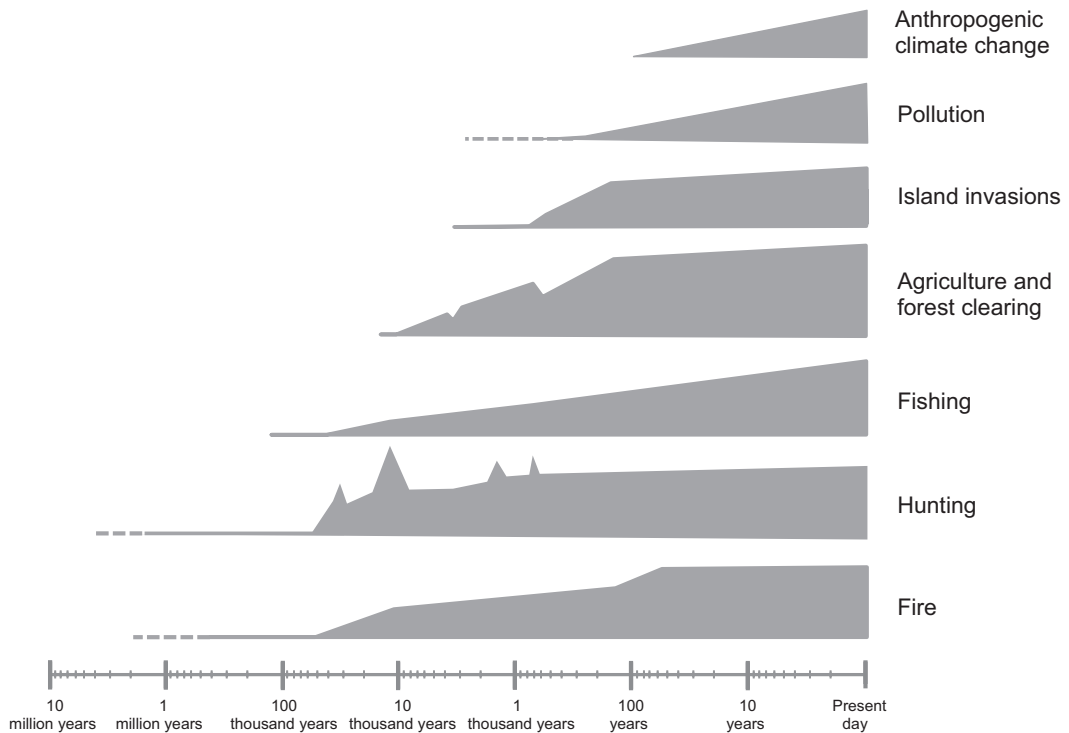


Figure 2

Qualitative representation of the temporal evolution of the main anthropogenic drivers of biodiversity change. References used for dating the pressure trend of each driver: fire (23, 24), hunting (28), fishing (160), agriculture and forest clearing (36, 40, 41), species invasions on islands (42), pollution (2), and anthropogenic climate change (138).

(28). Megafauna also went extinct in the large islands of Madagascar (e.g., giant lemurs) and New Zealand (e.g., ten species of moa) soon after human arrival at about 2,000 years and 1,000 years ago, respectively (22, 27). The relative roles of human hunting versus climatic changes in driving megafauna extinctions have been hotly debated (32), but it is now becoming accepted that, although climate may have contributed to preempt the conditions for the megafauna decline, humans played a major role in accelerating extinctions through hunting (27, 28). The megafauna extinction had major impacts in ecosystems, including on the fire regime, seed dispersal regime, and ecosystem function and structure (33, 34).

The next large-scale impact on ecosystems came with the development of agriculture (Figure 2) (35). There were multiple origins

of crop domestication: einkorn wheat, emmer wheat, barley, rye, lentil, pea, bitter vetch, chickpea, and flax, starting about 10,000 years BP in the Fertile Crescent (36); rice, soybean, and foxtail millet in East Asia at about the same time (37); and squash, peanut, quinoa, and cotton between 9,000 years and 6,000 years BP in parts of the Andes (38). Agriculture rapidly radiated from these regions to other regions occupied by humans, although at a faster rate in Eurasia than in the Americas or sub-Saharan Africa (39). But agriculture was not only the domestication of crops. Domestication of animals was a key component of the development of agriculture, particularly in the Fertile Crescent, where sheep, goats, and pigs started being domesticated around the same time as the plants (40). Over millennia, agriculture would bring major ecosystem changes with

the deforestation of large areas, changes in fire regime, the appropriation of primary productivity by humans, and the replacement of wild herbivores by domestic grazers (11, 28, 41). In Europe, by 3,000 years BP, perhaps as much as 30% of the usable land for crops and pasture had already been cleared (41), a pattern that would continue to intensify over the following centuries, only briefly interrupted by the Dark Ages (AD 500–700) and the black death (AD 1350). At the beginning of the Industrial Revolution, at around AD 1850, the usable land cleared for agriculture in Europe may have reached a peak of about 80% (41), much higher than what is currently observed.

The most recent wave of extinctions before the Industrial Revolution occurred in islands and was likely associated with the expansion of global trade via maritime routes (**Figure 2**). Between AD 1500 and 1800, all documented extinctions occurred on islands (42). Bird extinctions are particularly well documented for that period. The major drivers of bird extinctions have been, by decreasing order of importance, invasive species, overexploitation, and habitat loss (42). The effects of invasive species, such as cats, rats, and goats, included both direct predation upon the native birds or the degradation of their habitats (43).

4. RECENT TRENDS IN GLOBAL BIODIVERSITY CHANGE

In this section, we review what is known about global biodiversity change since the Industrial Revolution (mid-nineteenth century onward). Much of the emphasis is on very recent changes in the past 40 years, as some of the data are only available for that period. We divide our analysis into four different dimensions of biodiversity change that have different scores in the loss and alteration axes (**Figure 1**).

4.1. Species Extinctions and Extinction Risk

During the twentieth century, there were approximately 100 extinctions of birds, mammals,

and amphibians (16). Considering that there are approximately 21,000 species described in these groups, this yields a rate of 48 extinctions per million species years (E/MSY), about 20 to 40 times greater than the average extinction rate for the Cenozoic fossil record of 1–2 E/MSY (6). Unfortunately, much less is known for other taxonomic groups and for organisms inhabiting the marine (44) and freshwater realms (45). In the very recent period of 1984–2004, the International Union for Conservation of Nature (IUCN) recorded 27 extinctions (42). Approximately half of these extinctions have occurred on continents, suggesting that recent extinctions are no longer mostly restricted to oceanic islands. Twelve of the extinct species were flowering plants, followed by eight amphibians and six bird species. Habitat loss is thought to have played a role in 13 of these extinctions, followed by invasive exotics and disease (particularly the amphibian disease chytridiomycosis). Habitat loss seems therefore to be playing a much larger role in very recent extinctions than in previous centuries, and disease is emerging as a new threat (42).

The current importance of habitat loss and degradation is also apparent from analysis of the IUCN Red List of Threatened Species (**Figure 3**) (42, 43), where it is identified as the main current threat to amphibians, mammals, and birds. The Red List identifies not only the species that have been confirmed to have gone extinct but also the species that are currently threatened and, if pressures remain, may become extinct in the future. This allows for a more immediate analysis of global biodiversity change, as the lag between the initial decline resulting from a pressure, such as habitat loss, and the final extinction may take centuries or millennia (46, 47). Furthermore, a species may become functionally extinct with a major impact on ecosystem processes and services much before it becomes extinct in the wild: Examples include the disappearance of birds playing a major role in seed dispersal and pollination (48) and the collapse of fisheries (19, 49). The Red

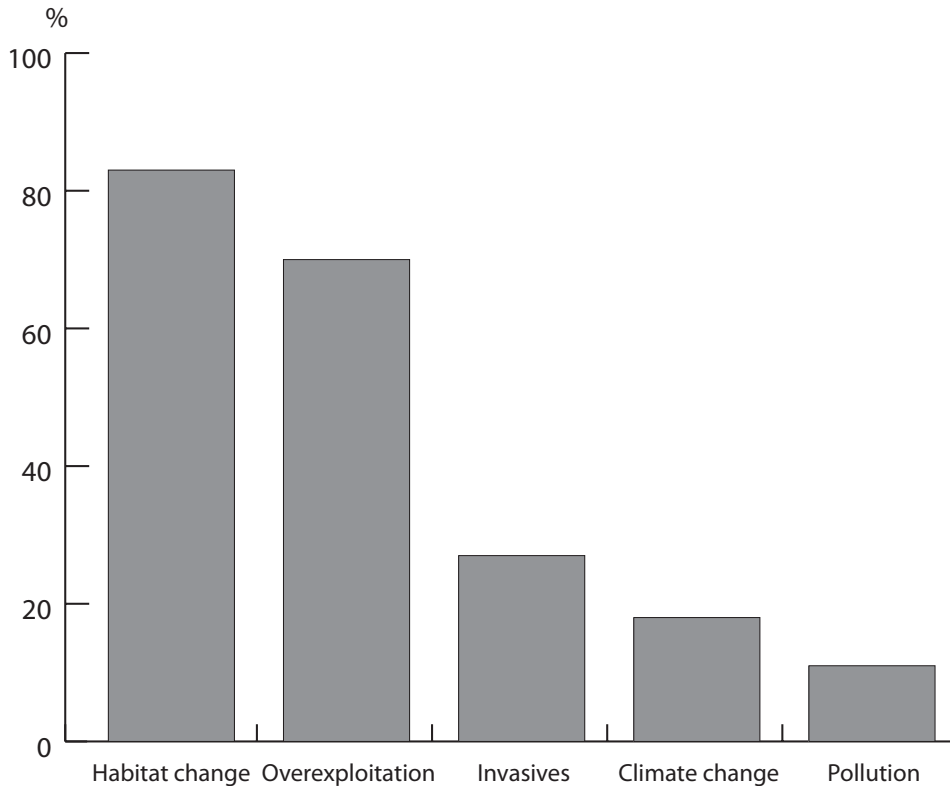


Figure 3

Proportion of threatened species affected by each driver. Threatened species ($n = 4,259$) include mammals, birds, and amphibians in the following Red List categories: critically endangered, endangered, and vulnerable. Main threats are classified as habitat change (i.e., residential and commercial development, agriculture and aquaculture, energy production and mining, transportation and service corridors, and natural system modifications), overexploitation, invasive species, climate change, and pollution (161). Several threatened species are affected by multiple threats.

List uses objective criteria to assess the degree of threat to a species into one of seven major categories of increasing risk (50): least concern, near threatened, vulnerable, endangered, critically endangered, extinct in the wild, and extinct. Species that have been assessed by the IUCN but for which insufficient data are available to define the threat category receive a data-deficient classification. Of the 30,738 species from taxa representatively assessed in 2010, 23% were threatened (**Figure 4a**), assuming that the proportion of threatened species for data-deficient species is the same for data-sufficient species. This is

a high proportion and reflects the seriousness of the biodiversity crisis. Nonetheless, it must be interpreted with care because the approach used to assess threat includes not only population and geographic range reductions (extrinsic factors), but also characteristics of the species, such as small population size and restricted geographic range (intrinsic factors). Species may exhibit these characteristics naturally, and they may not be correlated with human-induced extinction risk (51).

Another problem is the taxonomic bias of the assessed species. We still do not know how many species exist on Earth, with a

recent estimate placing the total number of species at 7.4 to 10 million (52). Of these, only around 1.7 million species have been described (**Figure 4a**) (16, 43). Systematic global Red List assessments have been carried out for only a few taxonomic groups, and the proportion of species assessed in each group is very different from its representation in global biodiversity (**Figure 4a**). It is virtually impossible to assess the extinction risk of all taxa. Instead, in the past few years, the IUCN has developed a randomized sampling approach to expand its assessment to more taxonomic groups (53).

Still, the overall pattern emerging from the Red List assessments is that amphibians (41% threatened) and cycads (63% threatened) are the most threatened groups, and birds are the least threatened group (13% threatened) (54). The generally low mobility and small ranges of amphibians and cycads may contribute to this vulnerability, but one might also ask if our better knowledge of bird species has contributed to their lower assessment of threat.

Most of the threatened terrestrial vertebrates occur in tropical regions (**Figure 5b**), following the latitudinal trends in the species richness of this group (**Figure 5a**). A very different map is obtained by looking at the relative proportion of threatened species in each grid cell (**Figure 5c**). Incidence of threatened species is high in much of Asia (except the North), the Sahara, the Andes, Madagascar, the Caribbean, New Zealand, and other islands. Areas of high species diversity and moderate to high incidence of threatened species include the Indo-Malayan region (particularly Southeast Asia), the Andes, Central America, the Brazilian Cerrado and Atlantic Forest, and some localized areas of sub-Saharan Africa (**Figure 6**). These are regions with restricted-range species (42, 55), and most have undergone rapid forest loss (56, 57).

The pattern for threatened marine vertebrates (cartilaginous fish) is somewhat similar, with higher occurrence of threatened species in the tropics, but there is also a strong coastal signal, with both of these regions having higher species richness (54). When one controls for

the species richness effect, high incidence of threatened species is still found at coastal areas (54). This pattern agrees with the higher human pressure on coastal regions, particularly that associated with fishing activities (15).

The Red List status gives us a snapshot of what is happening to biodiversity at a given time. However, we are also interested in understanding the trends in biodiversity. The Red List Index compares the proportion of species in the different threat categories over time (43, 54, 58). A key component of developing the Red List Index is the identification of species that have changed status not because more information became available but because the conservation situation of the species changed, i.e., genuine changes (43). Red List Indices have been calculated for birds (1988–2008), mammals (1996–2008), amphibians (1996–2008), and corals (1996–2008) (8, 54, 59). In all cases, the Red List Index shows an increase in the proportion of threatened species, and this increase is especially pronounced for corals owing to the large-scale bleaching event of 1996–1998. It is important to understand that a flat (or unchanging) Red List Index means, in theory, that species are still declining toward extinction, as the maintenance of a given category of threat indicates that a species population size or geographic range continues to decline at the same rate (60). This contrasts with the mean population abundance indices discussed in the next section, where a constant value means the maintenance of the relative extinction risk. However, the fact that the risk assessment includes both population/range size and population/range change can blur this distinction.

4.2. Changes in Species Abundances and Community Structure

Changes in extinction risk status can be slow and do not capture important alterations of ecosystem function that can occur when species abundances change (61, 62). In the past decade, several indicators have been developed to assess the population abundance dimension of

biodiversity (**Figure 4b**), including the Living Planet Index (LPI) (20, 63), the European Common Farmland Bird Indicator (64), the Wild Bird Index (WBI) (covering North America and Europe) (8), and the European Butterfly Indicator for Grassland Species (65). Most of the data in these indicators comes from extensive observation networks of volunteers (66), and they portray one of the most immediate and detailed pictures of global biodiversity change. The idea in each of the indicators is to obtain the average population trend across a set of species and their populations. For example, the LPI includes 7,190 vertebrate populations from 2,301 species across the marine, freshwater, and terrestrial realms (8). The LPI for a given year is based on the geometric mean across all populations of the relative abundance indices between that year and the previous year (i.e., $\frac{N_t}{N_{t-1}}$). That geometric mean is then multiplied by the value of the LPI in the previous year to give the final index value for that year, starting in 1970 with the value 1 (or 100%). The geometric mean of relative abundance indices has nice statistical properties, particularly when based on common species, and is able to detect overall abundance and evenness decreases and, to some extent, species richness decreases (67, 68). The geometric mean is equal to one when the halving of the density of a species is compensated by a doubling of the density of another species. The other indicators mentioned above follow similar approaches.

Overall, the pattern that emerges from all of these indicators is of global or regional declines of species abundances, despite some year-to-year fluctuations of some indicators (**Figure 4b**). The LPI has declined from 1970 to 2006 by 31% (8), the WBI for habitat specialists has declined from 1980 to 2007 by 2.6% (8), the European Common Farmland Bird Indicator declined from 1980 to 2006 by 49% (69), and the European Butterfly Indicator for Grassland Species declined from 1990 to 2009 by 70% (based on a best-fit line) (65). These numbers paint a depressing figure and are in some cases large enough to suggest that ecosystem processes and services are being modified (70, 71).

However, they must be interpreted with some caution as the spatial and taxonomic coverage of these indicators is limited (72). Furthermore, a finer analysis of these indicators can tell some contrasting stories. The tropical terrestrial LPI has declined, but the temperate terrestrial LPI has increased (20). One possible explanation is that, although tropical ecosystems are now undergoing fast and detrimental land-use change and overexploitation (2), these drivers peaked in temperate regions much before 1970 and are now decreasing as a consequence of farmland abandonment, greater species protection, and conservation actions. This has favored the return of large mammals (those that survived the earlier extinction wave) and other species in some temperate regions (17, 73). Still, the same habitat changes that have benefited large mammals are thought to contribute to the decline of farmland birds and grassland butterflies, although agricultural intensification is likely to play a major role too (64, 65). There are major geographic differences in the marine LPI, with strong decreases in the Indian Ocean and Southern Ocean and increases elsewhere (20). Similarly, although the terrestrial species in the Wild Bird Index have declined by 16%, the wetland species have increased by 40%. This last case also illustrates the problem of spatial coverage: The Waterbird Population Status Index, with global coverage and measuring the proportion of monitored shorebird populations, declined 18% from 1985 to 2005 (8). We discuss biodiversity change uncertainties associated with spatial coverage in detail in Section 6.

In the marine realm, much of the existing data come from fisheries, which have influenced the development of marine biodiversity indicators. The Marine Trophic Index (MTI) measures the mean trophic level of fish landings (74). The MTI declined globally in the 1960s and in the 1980s, and it increased in the early 1970s and since the 1990s (8, 75). Declines have been attributed to overfishing of large species, leading to shifting fishing efforts to smaller species at lower trophic levels. Recent increases have been attributed to the spatial expansion of the fishing effort (8, 76). The sensitivity of the

LPI: Living Planet Index

Biodiversity indicator: a metric used to assess the rate and intensity of biodiversity change

MTI to changes in the spatial distribution of fishing effort has led to the search for alternative measures of species abundance changes in the oceans. One such measure is the proportion of fish stocks not fully exploited or depleted (**Figure 4b**). For the fisheries that have been assessed, this proportion has decreased to half since 1974, and currently, only 21% of the stocks are not fully exploited or depleted (8, but see Reference 19 for an alternative estimate). Although the MTI and the proportion of fully exploited stocks give us a measure of the capacity of the ecosystem to provide a service, they may not reflect the overall state of biodiversity in those systems, as many species are not targeted by fishing.

Coastal habitats have been undergoing particularly high human pressure (77), and coral reefs, one of the most biologically diverse and productive systems on the planet, are particularly vulnerable because of their sensitivity to climate change and other pressures (78, 79). One measure of the community structure of coral reefs is hard-coral live cover (80, 81). Hard-coral live cover had a marked decline in the late 1970s in the Caribbean, following the white band disease outbreak, but has remained steady since the mid-1980s, although other community changes have been observed, including an increase in macroalgae cover in the late 1980s (**Figure 4b**) (81). In the Indo-Pacific live hard-coral cover has declined since the 1980s, and particularly from 1997 to 2004 (80), and in 2003, coral cover averaged 22.1%, a value much lower than the historic baseline estimates of >50% cover. The bleaching event of 1996–1998 has had major impact, but disease, sedimentation from coastal development, and destructive fishing practices have also played a role.

4.3. Shifts in the Distribution of Species and Communities

Climate change and other ecosystem change drivers may cause alterations in species distributions (3, 82, 83). The alteration of a species

distribution can be decomposed into two major aspects: directional shifts in the distribution (3) and changes in the size of the distribution (84). Directional shifts have been measured using species distribution centroids (3) or range limits (85). Recently, a new measure for directional shifts has been proposed, the Community Temperature Index, which tracks how the composition of communities at each site changes toward high-temperature dwelling species (86). Changes in the size of the species distribution are likely to be correlated with overall changes in species abundance (87, 88); however, directional shifts in the distribution may go undetected if only total species abundances are tracked.

An early meta-analysis of birds (United Kingdom), butterflies (Sweden), and alpine herbs (Switzerland) suggested that species were moving their range limits poleward at an average rate of 0.61 km/year (**Figure 4c**) (85), providing evidence of climate change impacts on species distributions. Another study analyzing northern limit shifts across 16 taxonomic groups in the United Kingdom found average shifts of 1.2–2.5 km/year (**Figure 4c**) (89). More recently, an assessment of distribution shifts for birds and butterflies in Europe, using the Community Temperature Index, has found rates of 2.1 and 6.3 km/year, respectively (**Figure 4c**) (90). The one order of magnitude difference between the lowest estimate of range shifts and the highest estimate may be caused by the different methods used, the different regions, and the different taxa analyzed. The intervals of species shift rates are consistent with those of the velocities of isotherms from 1960 to 2009 in land surfaces (median of 2.7 km/year) and oceans (2.2 km/year), which exhibit large spatial variations, with some regions exhibiting no significant shifts and others shifting at rates higher than 10 km/year (91).

Average shifts may hide substantial variation in individual species responses, as some species maintain their previous ranges, others move toward the poles (i.e., North in the Northern Hemisphere), and yet others move in

unexpected directions (83, 92). For instance, in the North Sea, the varying responses of different species (**Figure 4c**) led to a nonsignificant change in the mean latitude of species ranges from 1980 to 2004, although most species assemblages tracked yearly fluctuations in climate with mean latitudinal shifts of 10–70 km/°C (83). Some species assemblages, such as warm-water specialists, exhibited significant overall shifts during these 25 years, moving northward at a rate of 4 km/year (83).

Species can also adapt to climate change by shifts in elevation (85, 92) or depth (83), shifting life history traits in time (93), or by adapting to the new conditions in their local range through phenotypic plasticity or microevolution (94).

4.4. Genetic Diversity in Domesticated and Wild Species

Of the four biodiversity dimensions analyzed here, we have the least information at the global level for changes in genetic diversity. Studies of loss of genetic diversity can be classified into two categories: studies of genetic diversity of domesticated species and studies of genetic diversity of wild species. Studies of domesticated species can further be divided into plant genetic resources (95) and animal genetic resources (96).

Over the past few decades, the worldwide adoption of modern crop varieties adapted to high-input systems has led to the reduction in the area farmed with local crop varieties (95). This change in agricultural practices has raised concerns: For instance in China, the number of rice breeds in production is reported to have declined since the 1950s from 46,000 to 1,000, and most of the 10,000 traditional corn breeds are no longer in production (97). Still, there are many farm communities that, although exposed to modern varieties, choose to maintain, at least in portions of the farm, traditional varieties (98). The picture of allelic diversity change is also complex. Although some studies report declines in allelic diversity of modern varieties over the past few decades (99), a meta-analysis

of 44 studies has found no significant overall trend (100). Another concern is the status of the crops' wild relatives, which are under the same threats as other aspects of biodiversity, and recently a system of priority areas for their conservation in situ has been proposed (95).

Of the about 7,600 animal breeds (among 36 domesticated mammal and bird species) registered in the UN Food and Agriculture Organization's Global Databank, 20% are classified as being at risk, and a further 9% have become extinct (**Figure 4d**) (96). Over the past decades, a similar phenomena to what happened with the crop varieties is occurring with the animal breeds: Local animal breeds are being replaced by widely used and high-output breeds more adapted to intensive animal production systems (7).

Less is known about the loss of genetic diversity in wild populations. One study has estimated that about 16 million populations are being lost annually, on the basis of an estimate of 220 populations per species derived from a review of population genetic studies and an assumption of linearity between tropical deforestation and population extinction rates (101). This is a very indirect estimate, and to our knowledge, it has not been confirmed independently. Other studies have looked at patterns of genetic diversity in populations impacted by humans (102, 103). A meta-analysis of population genetics studies found decreases in genetic diversity in animal and plant populations under pressure of habitat fragmentation and no consistent signal for populations affected by hunting or fishing, but found diversity increases in populations affected by pollution (103). Another meta-analysis, targeted only at mammals, found significant lower genetic diversity in mammalian populations that have experienced a reduction in population size or range or a population bottleneck (102). In a rare longitudinal study, Lage & Kornfield (104) looked at the genetic diversity in a population of the Atlantic salmon (*Salmo salar*) using samples from 1963 to 2001. They found

that genetic diversity declined during this period, closely following population declines.

5. UNDERSTANDING THE DIRECT PRESSURES

We now examine five major categories of global biodiversity change pressures. For three of those, habitat change, pollution, and climate change, global models of their impacts are available, and we make comparisons between the terrestrial spatial pattern of the driver and the impacts on species extinction risk (**Figure 7**). Note, however, that the current biodiversity impacts of land-use change are much greater than the impacts of the other two drivers (**Figure 3**).

5.1. Habitat Change and Degradation

Habitat change and habitat degradation are currently the major drivers of global biodiversity change (**Figure 3**). In terrestrial systems, land-use change dynamics can be broadly classified into three categories: conversion of natural habitats to human-dominated habitats, intensification of human use of human-dominated habitats, and recovery of natural vegetation and forest in areas that have been previously cleared by humans. Not all species respond equally to habitat changes (105–107): When forest is converted to agriculture and pastures, some species may increase in abundance, whereas other species, particularly habitat specialists (108, 109), can decline or even go locally extinct.

Although the three types of land change dynamics occur in most world regions, the relative importance of each one has a strong latitudinal pattern (**Figure 7b**) (2, 110): Most conversion of natural to human-dominated habitats is occurring in tropical forests (111); agricultural intensification started in the developed regions but is rapidly expanding to the rest of the world (not represented in **Figure 7b**) (112); most recovery of natural and forest vegetation is occurring in temperate regions in Europe and North America (17) (**Figure 7b**). A net forest loss of about 42,000 km² per year (111) in tropical

regions is partially balanced by a net forest gain of 8,700 km² per year in Europe (110). However, part of the net forest gain is the result of new forest plantations, often with exotic species, which often have lower biodiversity than natural forests (113). Fire plays a major role in many regions in the conversion of forest to agriculture but also in maintaining open landscapes.

As expected, there is an agreement between the spatial distribution of areas of natural habitat being converted to agriculture and the distribution of species affected by habitat loss (**Figure 7a,b**), including in Madagascar, some areas of sub-Saharan Africa, Brazil's Atlantic Forest, the Middle East, and Southeast Asia. Forest loss in Southeast Asia is not well captured in our land-use change map but has been reported in other studies (57). There are some regions where there is a high proportion of species affected by habitat loss where most land-use change already occurred in the past (much of Europe), and regions where species have been affected by habitat loss not captured in our analysis (e.g., the Sahara).

River systems have been deeply altered by impoundments and diversions to meet water, energy, and transportation needs of a growing human population (14). Today, there are more than 45,000 large dams (>15 m in height) worldwide (14). Dams have upstream impacts, where lotic systems are changed into lentic systems, and downstream impacts, where the timing, magnitude, and temperature of water flow is changed (45). Dams are also responsible for the fragmentation of river systems, as they hamper or even block the dispersal and migration of organisms (14). Furthermore, water resource development by impoundments and diversions has high spatial overlap with other pressures in freshwater ecosystems, such as pollution and catchment disturbance by cropland (114). Other important habitat changes in freshwater ecosystems include the loss of wetlands owing to drainage for conversion to agriculture or urbanization, overextraction of groundwater (45), and the excavation of river sand (115).

Marine habitats are also being affected by human activities, particularly by destructive fishing practices, such as trawling and dynamiting (116). Coastal habitats and wetlands have been affected mostly by urbanization, aquaculture development, and coastal engineering works (15, 77).

5.2. Overexploitation

Overexploitation is the major driver of biodiversity loss in the oceans (2, 19). Capture fisheries production increased for much of the twentieth century but has reached a plateau since the mid-1980s at around 70–80 million tons annually, despite continuing increases in global fishing effort levels (117, 118). The global landings would have likely declined except for the spatial expansion of the fishing effort toward deeper and further offshore waters. By the mid-1960s, most fully exploited or overexploited fisheries were located in coastal areas of the Northern Hemisphere. By the 1980s, fishing efforts were having an impact on regions much farther away from the coast, in the middle of the northern and southern Atlantic Oceans. One decade later, the spatial expansion of the fisheries had reached much of the world's oceans, with only some parts of the Indian Ocean, the Pacific Ocean, and the Antarctic ocean not having reached maximum historical catches (116).

In terrestrial systems, hunting is a major concern in tropical savannahs and forests (2). Large birds and mammals are targeted for their meat and charismatic species for their ornaments and alleged medicinal purposes (108, 111). Wild-meat harvest has been estimated at 67–164 thousand tons in the Brazilian Amazon and 1–3.4 million tons in Central Africa (119). The impacts are particularly acute in Southeast Asia and Central Africa (111). A connection has been established between the reduction of fish availability per capita and the increase in hunting pressure of wild meat in West Africa (120). Synergistic interactions between hunting and other drivers, such as land-use

change and disease, can also occur and cause local extinctions (106).

5.3. Pollution

Eutrophication and other ecosystem changes caused by pollution are major drivers of biodiversity loss and alterations in both inland waters and coastal systems (121). River nitrogen loads from point sources, such as domestic and industrial sewage, and nonpoint sources, such as agriculture and atmospheric deposition, increased in most world regions from 1970 to 1995 but are starting to decline or are projected to decline until 2030 in Europe and northern Asia (Russia) (122). Lakes are particularly vulnerable to regime shifts caused by eutrophication, which may be difficult to reverse (47, 123). Eutrophication can lead to increased biomass of phytoplankton and macrophyte vegetation, blooms of toxic cyanobacteria and other algae, higher incidence of fish kills, and, in the case of coral reefs, declines in coral reef health and loss of coral reef communities (121).

Atmospheric nitrogen deposition from intensive agriculture and fossil-fuel combustion can also affect terrestrial ecosystems, particularly temperate grasslands (2). The increase in availability of nitrogen changes the competition dynamics in plant (124) and lichen communities (125), favoring the increase of nitrophilous species and the decline of nitrogen-sensitive species. One study found a linear relationship between the rate of nitrogen deposition and species richness declines in temperate grasslands and estimated that, for the levels of nitrogen deposition observed in much of central Europe (17 kg/ha/year), a 23% reduction of species diversity can be expected (124). Unfortunately, some high species diversity regions (e.g., Southeast Asia and Brazil's Atlantic Forest) are also receiving similar levels of nitrogen deposition (**Figure 7d**), but more research is needed to identify its impacts (126). A visual inspection of the spatial overlap between the global patterns of nitrogen deposition and the distribution of vertebrates affected by pollution shows reasonable

agreement in Europe, but inspection also shows disagreement in other parts of the world, such as Central Africa (**Figure 7c,d**). Note, however, that there are other sources of pollution included in the assessment of species extinction risk (**Figure 7c**) and not directly related to atmospheric nitrogen deposition (**Figure 7d**).

5.4. Introduction of Exotic Species and Invasions

One of the major trends in global biodiversity change is the increased homogenization of plant and animal diversity owing to biotic exchange. In some cases, exotic species are able to spread beyond the places where they were introduced, spreading in the landscape and out-competing native species (127). Islands have been particularly affected by invasive species (128): Animal invasions have led to species extinctions, whereas plant invasions can decrease the abundance of native species and become dominant in plant communities. Plant invasions may also affect the nutrient cycles, alter the fire regimes, and impact other ecosystem services (129, 130). A particularly serious type of invasions is epidemic disease. One example is chytridiomycosis, which has been decimating amphibians in many regions of the world and is a leading cause of the global amphibian decline (131). Invasive species have also had important impacts on freshwater ecosystems, where their incidence is correlated with human economic activity (132), and in marine and estuarine ecosystems due to ballast water or hull fouling transported by ships (133).

Still, many invasive species have had more moderate impacts on ecosystems (134), and recently, some ecologists have called for a more embracing attitude toward exotic species, arguing that alien species should not be a priori considered negative in an ecosystem but should be assessed objectively for their impacts (135, 136). Others have argued for active translocation or assisted migration of species endangered by climate change (137), an approach that seems fraught with peril on the basis of our

historical experience of human introductions of exotic species, often with the best intentions.

5.5. Climate Change

Global mean surface temperature increased 0.74°C from 1906 to 2005 and is expected to increase between 1.8°C and 4°C during the twenty-first century, depending on the socioeconomic scenario (138). Warming is spatially very heterogeneous as it is largest in terrestrial systems and at high northern latitudes, with recent warming greater than 1.5°C in some areas, and least pronounced in the tropics, where many regions have warmed around 0.5°C (**Figure 7f**). The impacts of climate change are already contributing to increased extinction risk of species at high northern latitudes (**Figure 7e**). Further climate change impacts in these regions have been projected for birds (139) and for plants (46) during this century. Surprisingly, in the Cape region (South Africa) and in southeastern Australia, a high incidence of species negatively affected by climate change has been reported (**Figure 7e**), although these areas are not suffering large warming (**Figure 7f**). One explanation may be that those regions have many species particularly vulnerable to climate change. Species with high vulnerability are species that have narrow climate niches, cannot shift their ranges, or are unable to change their phenology, evolve their physiology, or behaviorally adapt to the new conditions (93, 140). For instance, the limited ability of mountaintop species to shift in elevation has been identified as a major climate vulnerability (92).

For amphibians, important future climate impacts have been projected in the northern Andes, parts of the Amazon, Central America, southern and southeastern Europe, sub-Saharan tropical Africa, and Southeast Asia (140, 141). Surprisingly, this disagrees somewhat from the recent spatial patterns of increased extinction risk owing to climate change (**Figure 7e**).

In corals, most threatened and climate change-susceptible species occur in Southeast

Asia (140). Climate change is also causing sea-level rise and threatening coastal habitats, particularly in synergy with land-use change, which may not allow coastal habitats to migrate inland (47). Marine ecosystems are also affected by ocean acidification caused by climate change, particularly corals (79) and other marine organisms that build calcium carbonate skeletons (142).

6. EXPLORING THE UNDERLYING CAUSES WITH SCENARIO MODELS

Upstream from the direct pressures on biodiversity, there are indirect drivers of biodiversity change. Major indirect drivers for biodiversity include population growth, energy use and energy production, diet, and food demand. Naturally, these drivers interact between them and with other drivers, such as technology development, socioeconomic changes, and cultural transformations (143). One way of exploring the relationship between the indirect drivers and global biodiversity change is through scenario modeling. Biodiversity scenarios have recently been reviewed elsewhere (3). They can be developed in three steps: (a) plausible trajectories of key indirect drivers are generated; (b) the trajectories are fed into models that project changes in direct pressures; and (c) projected pressures are used as inputs of biodiversity models. Many scenarios explore different futures and how they depend on policy decisions, but scenario models can also be used for hindcasting, i.e., to reconstruct the past.

The human population increased from 2.5 billion people in 1950 to 7 billion in 2011 and can reach between 8.1 billion and 10.6 billion people in 2050, depending on the scenario (144). The increase in human population growth is being accompanied by an increase in the demand for food (with food production growing faster than human population) and an increase in energy consumption (2). How much of the increase in food production needed over the next few decades will come from intensification or from farmland

expansion to natural habitats will depend on technological developments, policy choices, and societal behavior. Similarly, how a growing energy demand will be satisfied by additional fossil-fuel consumption or by shifting energy production toward other sources has also been explored in scenarios.

Most scenarios project a decrease in forest area by 2050 of up to 20% and in an extreme case, of more than 60% (3). Still, some scenarios that account for policies recognizing the role of forests in CO₂ sequestration and avoiding the impacts of land-use changes, including conversion of forests to biofuels, project net increases in forest area (3). Species extinction rates will continue to be higher than in the fossil record. For the same modeling approach, scenarios with lower levels of population growth and climate change result in lower estimates of biodiversity loss.

7. A BIT OF GOOD NEWS FOR A CHANGE

Despite the gloomy biodiversity picture depicted in the previous sections, there is also some good news about global biodiversity change due to the reversion of the effect of a driver (e.g., forest recovery) or the successes of conservation initiatives on the status of species (Table 1).

Measures such as habitat conservation, reintroduction programs, and legislation have proven to be efficient in improving the status of several species (145). One way to assess conservation successes is to identify prevented extinctions. Between 1994 and 2004, 16 bird species would have gone extinct if actions had not been undertaken to protect them (146). One example is the population of the Norfolk Island green parrot (*Cyanoramphus cookii*), very likely to go extinct in 1994, with only four breeding females, which has now close to 300 individuals thanks to habitat protection and control of predator and competitor species. In Europe, a comparison of bird population trends between Birds Directive Annex I (higher protection level) and non-Annex I species

Table 1 Examples of successful outcomes of global, regional or national conservation initiatives (expanded from References 8 and 54)

Successes ^a (references)	Detail/examples
Improvement in the Red List classification of species (8, 54, 145)	Mammals: 24–25 species out of 195 between 1996 and 2008 (1 species for every 7 with decreasing status) Birds: 33–44 species between 1988 and 2008 Amphibians: 4–5 species between 1980 and 2004 The improvement in the conservation status of these species is explained by habitat protection, reintroduction programs, legislation, control of competitors, or a combination of those measures.
Impact of the Bird Directive in Europe: Annex I listing (147)	Birds: significantly higher population trends for the 1990–2000 period when comparing Annex I and non-Annex I species.
Prevention of species extinction (146)	Birds: extinction was avoided for 16 species classified as critically endangered by the IUCN. The mean population size for these species was augmented from 34 individuals in 1994 to 147 in 2004. Conservation measures included habitat-based protection, invasives control, captive breeding, and (re)introductions.
Natural recolonization and recovery from local extinctions (153)	Mammals: increasing population size and distribution for carnivore species between 1970 and 2005 in Europe, following land abandonment and reduced human pressure: Gray wolf (<i>Canis lupus</i>) from 8,000 to 18,500 individuals; Brown bear (<i>Ursus arctos</i>) from 10,000 to 14,000 individuals; and Eurasian lynx (<i>Lynx lynx</i>) from 4,000 to 8,000 individuals.
Increased Water Quality Index (8)	This index of the physical and chemical quality of freshwater increased 7.4% in Asia between 1980 and 2005.
Restored fishery stocks (19)	In parts of the coasts of Australia, Canada, Iceland, New Zealand, and the United States, recovery of fishery stocks was made possible by the implementation of management programs designed to lower fishing pressure, to prevent overfishing, and to restore marine ecosystems.
Decreased pressure on forests (8)	In 2008, the annual area deforested in the Amazonian forest of Brazil represented less than half of the area cleared in 2004 (1.3 million ha versus 2.8 million ha). Nonetheless, it is not clear whether this decrease is due to legislation or to less demand for natural resources.
Conservation status and population trends in the EU25 (148)	Birds: 12 species (out of 448) no longer have an unfavorable conservation status (228 in 1990 versus 216 in 2000). Increasing population trends were also observed for species in marine, coastal, inland wetland, and Mediterranean forest habitats.

^aAbbreviations: EU25, European Union member states as of 2004; IUCN, International Union for Conservation of Nature.

(lower protection level) also shows significant differences, highlighting the effectiveness of the European policies (147). The conservation of threatened habitats, such as inland wetlands and Mediterranean forests, also allowed for an increase in some bird populations trends (148). At a global scale, Hoffman et al. (54) identified 68 species, including 40 birds, 4 amphibians, and 24 mammals, that showed an improvement in their conservation status, leading to a revision of their IUCN category.

In the marine biomes, the restoration of fishing stocks can deliver important benefits (19).

Conservation successes are also associated with the implementation of protected areas. Protected areas considerably increased during the past century and now cover 12% of the terrestrial surface (8). However, designations of protected areas do not always lead to the implementation of on the ground effective measures to protect habitats and species (149). Complementary tools to combat declines of biodiversity

outside nature reserves are agri-environment schemes, which are policy tools with ample scope to reverse the negative trends of once-common, widespread species (150), and direct payments to conserve biodiversity (151).

In some regions of the world, a habitat conservation strategy that is emerging as a significant opportunity is the rewilding of abandoned areas (17). Natural revegetation in large areas has been observed in the past and is predicted to occur in the next decades (**Figure 7b**), particularly on remote and marginally productive areas (e.g., mountains) in the Northern Hemisphere where agriculture and forestry activities are being abandoned (46, 152). The subsequent reappropriation of the land by wildlife can be beneficial for various species that take advantage of the reduced human pressure (17): Several European carnivores have been coming back to countries where they were previously extinct (153). Still, natural regeneration presents certain challenges that depend on the level of resilience of the land (154, 155) and potential conflicts with human populations (17).

Finally, aside from avoided extinctions and increasing population trends, conservation successes can be measured in changes in societies' behavior regarding sustainable resource uses. The increasing public support for biodiversity conservation in the past few decades (156), the commitment of the Convention on Biological Diversity parties to new goals for 2020 (157), and the recent establishment of the Intergovernmental Platform on Biodiversity and Ecosystem Services (<http://www.ipbes.net>) give hope of further progress in the years to come.

8. MAJOR GAPS IN OUR UNDERSTANDING OF GLOBAL BIODIVERSITY CHANGE

In this article, we reviewed the current scientific knowledge about the state of global biodiversity change. Overall, the patterns that emerge allow us to state with confidence that biodiversity is being rapidly altered on land,

in rivers, and in oceans, and is being lost locally in many regions and also globally. Some conservation actions have been successful at mitigating or, in a few cases, reversing biodiversity loss. However, many unknowns remain, and we still do not know the exact dimensions of the biodiversity crisis.

Some of the biodiversity indicators that were described in Section 4 and that were used to assess the 2010 target of the Convention on Biological Diversity are far from being completely developed (149). Very little is known about trends in genetic diversity, particularly in wild species. The taxonomic coverage of the indicators and assessments is very limited: The extinction risk of the vast majority of biodiversity is not known (**Figure 4a**), and most of the population indicators are derived from vertebrate populations (**Figure 4b**). This is not to say that the same conservation and research emphasis shall be placed on all biodiversity. People place high existence values on vertebrates (158), and many important ecosystem services are associated with vertebrates (48, 62). It is just an acknowledgment of the large gap in our taxonomic knowledge of global biodiversity change. More worryingly, even the available information for vertebrates is spatially very heterogeneous (72) and is least available in regions that are currently under pressure (**Figure 8**). The Group on Earth Observations Biodiversity Observation Network (GEO BON) aims at filling these gaps by integrating biodiversity monitoring programs across the globe and promoting biodiversity monitoring in gap regions (159).

Major gaps and uncertainties remain in modeling global biodiversity change. In terrestrial systems, most research has been dedicated to model climate change impacts, although some work has also been done on modeling the impacts of land-use change and, to a lesser extent, pollution. Models are lacking for the global spatial distribution of exploitation pressure and invasive species and their impacts in terrestrial systems. But even for the pressures that have received most attention, large uncertainties remain: Projected extinction rates for this century range from less than 20 E/MSY

to more than 14,000 E/MSY (3). Both the lack of harmonization of modeling approaches and the lack of knowledge of how species respond to global change contribute to this uncertainty.

9. IS ALL BIODIVERSITY CHANGE EQUALLY BAD?

Our world is changing, and biodiversity is no exception. Yet, not all biodiversity change is inherently bad, and we should avoid a static view of conservation biology (despite its name). The maintenance of the landscapes or the biological communities we know should not be the *a priori* management target. We need to assess biodiversity change with objective criteria. The ecosystem services framework (2, 70), with the appropriate inclusion of species existence values (158), is an excellent tool to assess the management priorities for biodiversity change. It allows us to identify not only the benefits and costs of biodiversity alterations for human well-being but also to prioritize the biodiversity losses that are more important to address.

Biodiversity alterations and losses have to be assessed for their contribution to ecosystem processes, such as nutrient cycling and soil formation, and to ecosystem services, such as climate regulation, water quality regulation,

water provisioning, timber provisioning, disease and pest regulation, and cultural services. An appropriate inclusion of existence values is essential; people place large values on the conservation of particular species or taxonomic groups. Therefore, not all species extinctions can be treated equally from a utilitarian point of view. The extinction in the wild of the viruses variola major and variola minor, the causes of the deadly smallpox, was arguably a good thing. But in many more cases, the loss of biodiversity is impoverishing us and making our planet more unequal for its human inhabitants: It is often the poor that suffer the first negative impacts of biodiversity change (2).

Some biodiversity alterations, such as the conversion of the Amazon forest to agricultural areas, may lead to tipping points in ecosystems that are hard to reverse (47), but the majority of biodiversity alterations are reversible through management. In contrast, biodiversity loss is usually irreversible: Extinction is forever, at least with the current biotechnology level. Scientists can inform society about how biodiversity is changing and what the likely consequences of those changes are for ecosystems and for human well-being, but it is up to society to decide what should be done about these issues.

SUMMARY POINTS

1. Biodiversity change is composed of biodiversity loss, such as species extinctions, and biodiversity alterations, such as species range shifts.
2. Biodiversity is changing at unprecedented rates in human history: Species are becoming extinct or closer to extinction; mean species abundances of several taxa are decreasing; species are shifting their ranges in response to climate change; and domestic and wild genetic diversity are being lost.
3. The major direct drivers of biodiversity change are habitat change and overexploitation. Pollution, exotic species, and disease are also important drivers. Climate change is an emerging driver of biodiversity change.
4. Human population growth and human resource use are the underlying indirect drivers of biodiversity change.

5. There have been some important successes in biodiversity conservation—mainly through species management, protected areas, and increased societal awareness. Farmland abandonment is an opportunity for biodiversity restoration.
6. Not all biodiversity change is bad. Biodiversity change should be assessed in relation to its consequences for ecosystem services and species existence values.

FUTURE ISSUES

1. There are major gaps in our knowledge of biodiversity change, and there is the need to improve our biodiversity monitoring programs worldwide.
2. There are also important uncertainties and gaps in our models of global biodiversity change.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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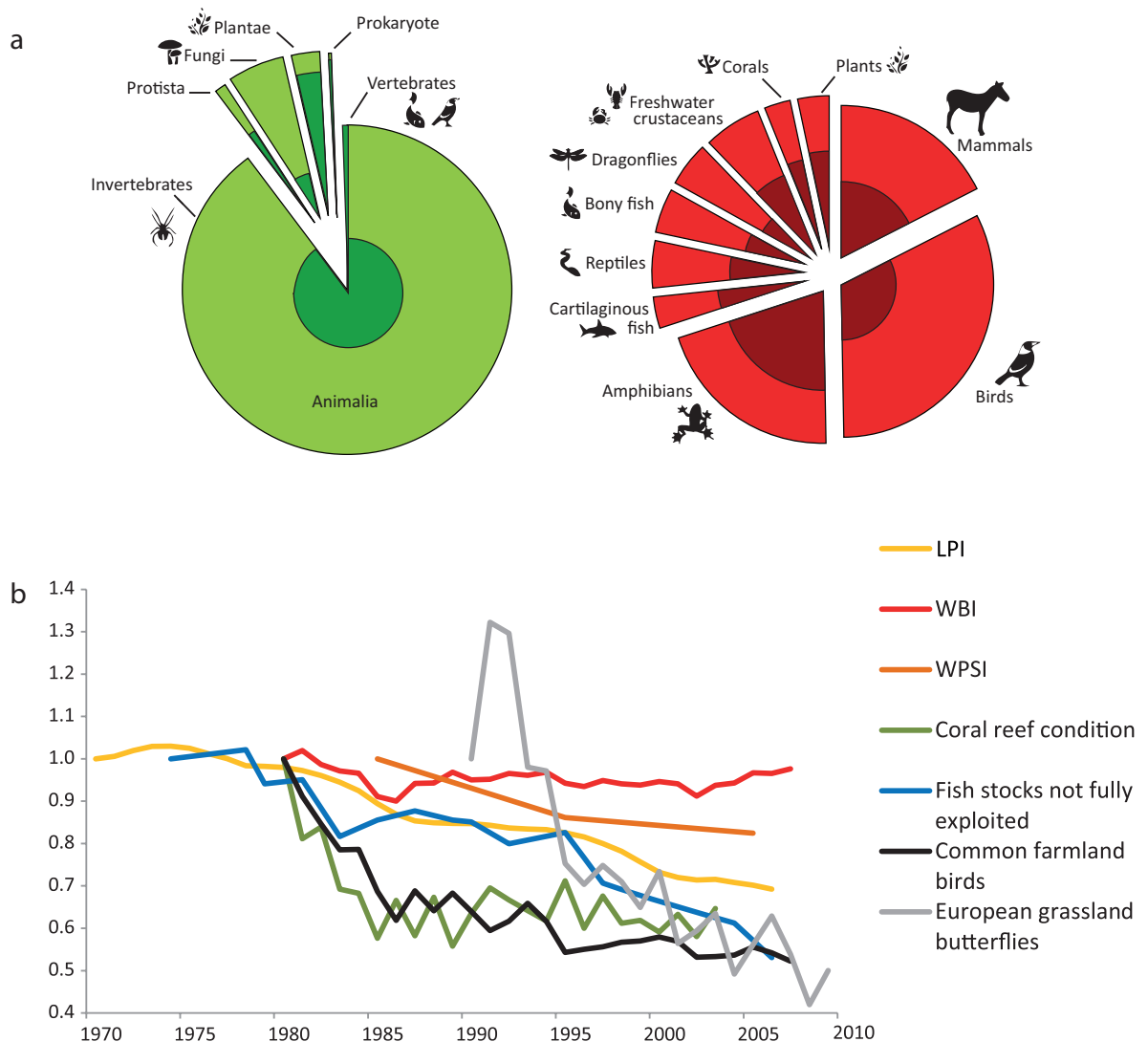


Figure 4

(a) (left) Estimated proportion of species in each of the main domains (52). For each taxonomic group, the dark green identifies the proportion of species already described relative to the estimated number of species. (right) Proportion of assessed species for each taxa that has been representatively evaluated by the IUCN (plants include cycads, conifers, and sea grasses; freshwater crustaceans include crayfish and crabs). The dark red identifies the proportion of species threatened in each group (54). (b) Evolution of some of the main biodiversity indicators between 1970 and 2010 (8, 162, 163). All indicators are dimensionless as they are scaled relative to their values in the first year for which information is available. (c) Observed northward shifts in species or communities of species (km/year): ① meta-analysis of shifts of the northern range limit for 99 species of butterflies, birds, and alpine herbs in Europe (mean \pm standard error) (85); ② northward shift in the composition of bird and butterfly communities in Europe (mean \pm standard error) (90); ③ mean shift of the northern range limit for 16 taxa in the United Kingdom, based on heavily recorded atlas cells (lower bound), well-recorded cells (middle line), all recorded cells (higher bound) (89); ④ mean shift of the northern range limit for 28 species of bottom-dwelling fishes in the North Sea, for all species (middle line), for warm specialists (upper bound), and for cold specialists (lower bound) (83). (d) Risk status for breeds of mammalian (5,600 breeds) and avian (2,000 breeds) domesticated species (96). The “at risk” category includes critical, critical-maintained, endangered, and endangered-maintained species. Abbreviations: LPI, Living Planet Index; WBI, Wild Bird Index (of habitat specialists); WPSI, Waterbird Population Status Index.

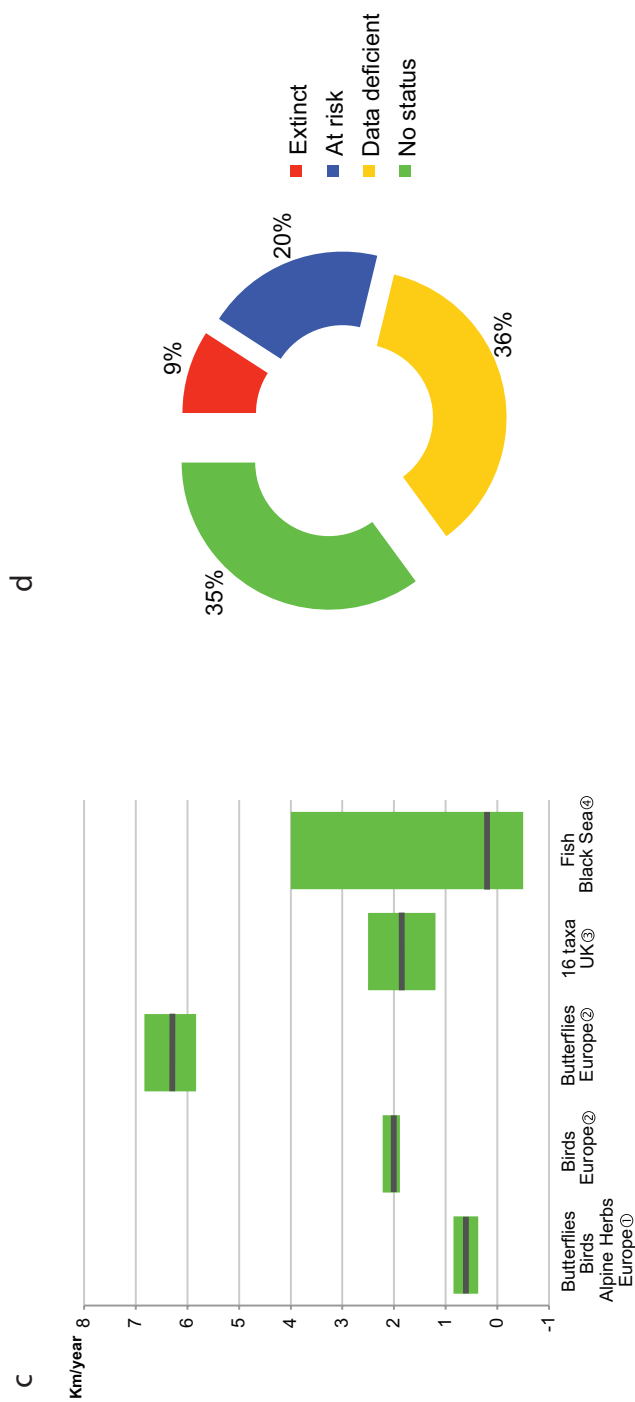
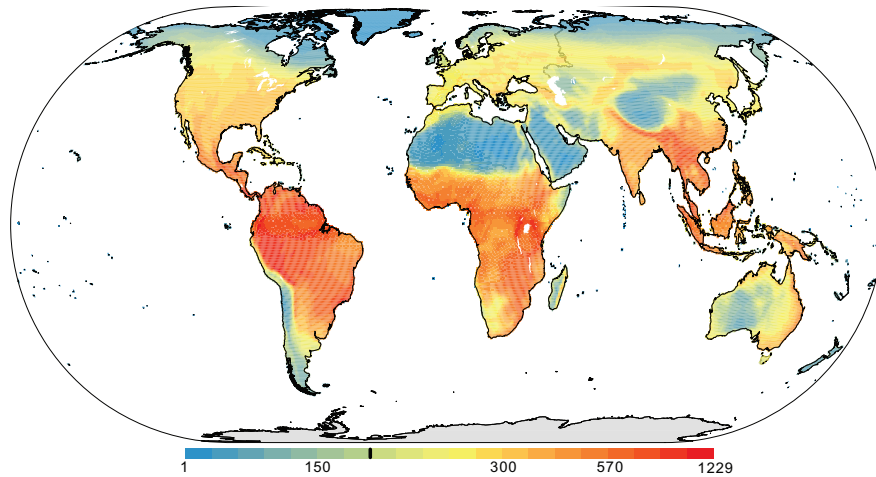
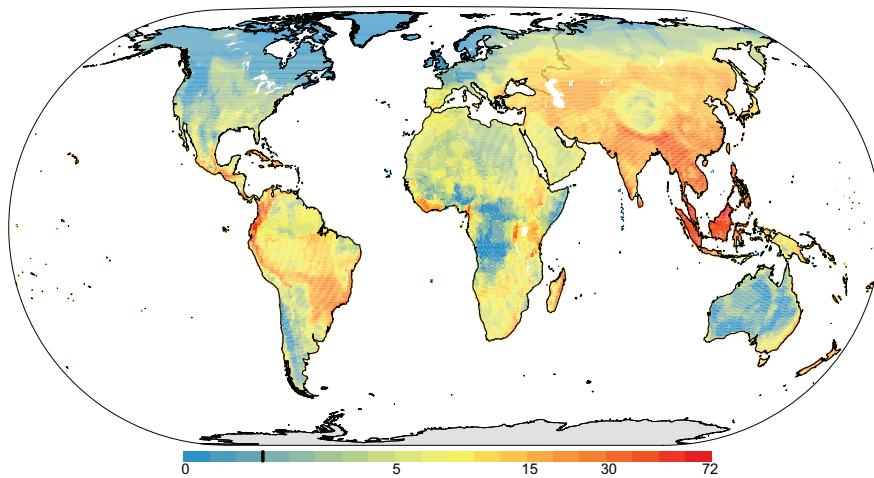


Figure 4
(Continued)

a



b



c

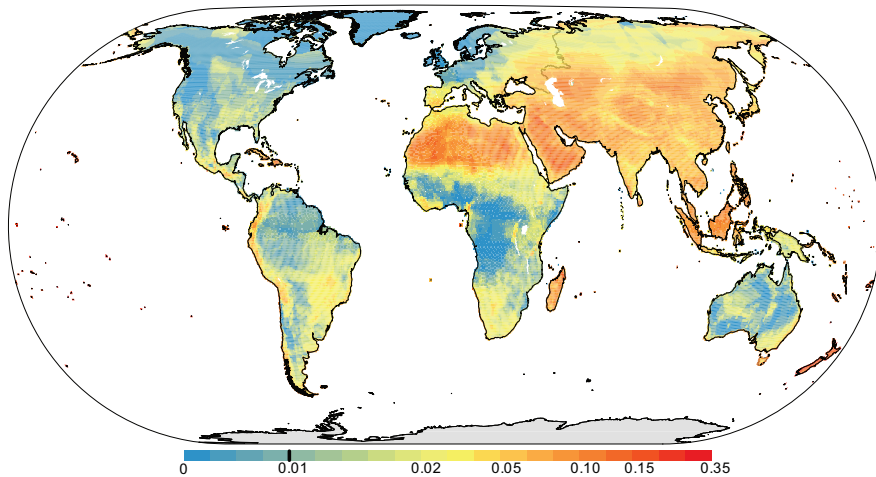




Figure 5

Global distributions of terrestrial vertebrates and threatened species, based on species ranges for birds ($n = 10,606$) (164), mammals ($n = 5,348$), and amphibians ($n = 6,248$) (161). Color scales are based on geometric intervals (interval size increases at a constant ratio to the left and to the right of the black bar in the scale). Density calculations are based on grid cells of $0.48^\circ \times 0.48^\circ$. (a) Species richness. (b) Number of threatened species (critically endangered, endangered, or vulnerable). (c) Proportion of threatened species (number of threatened species divided by number of species in each cell).

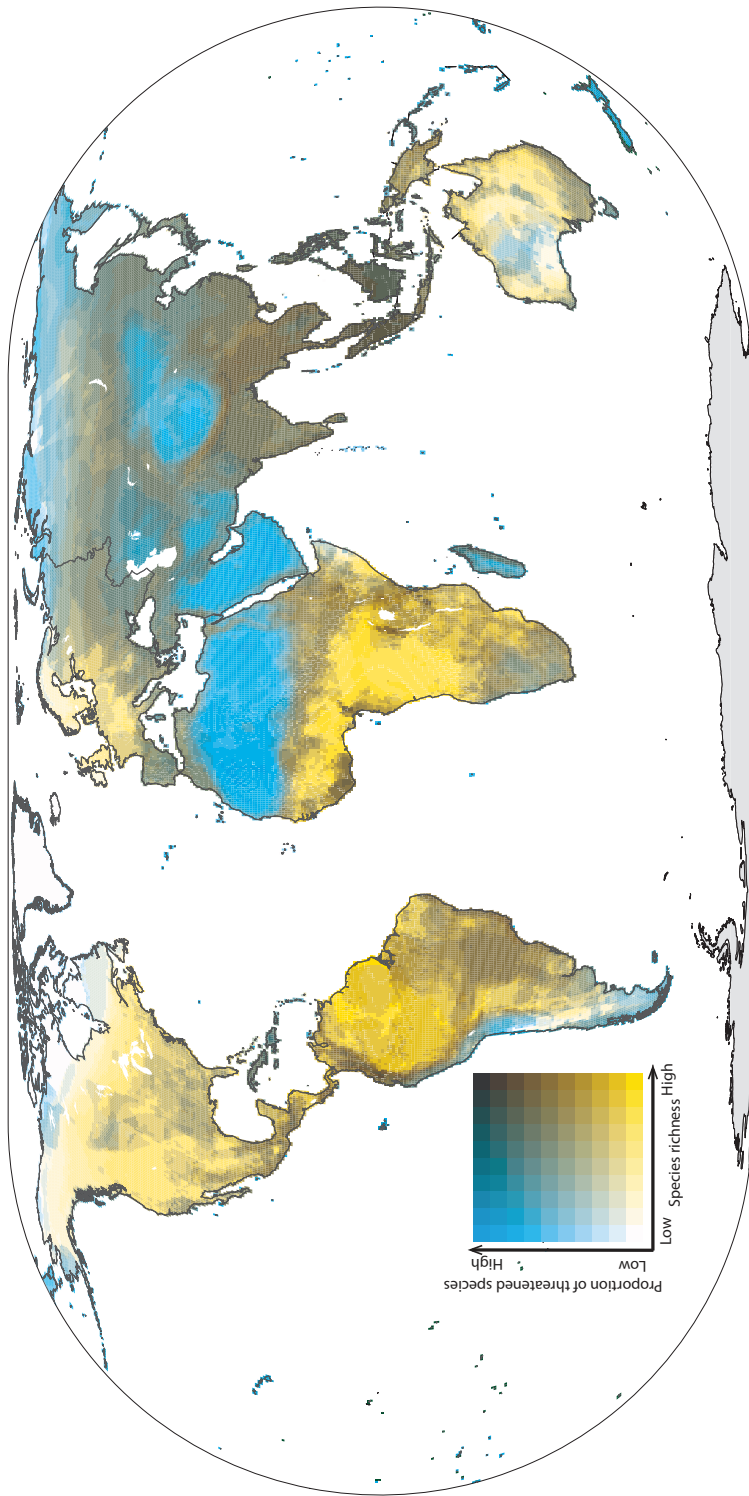
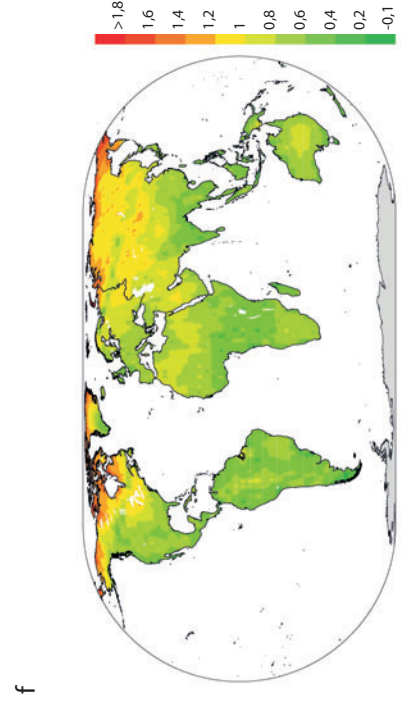
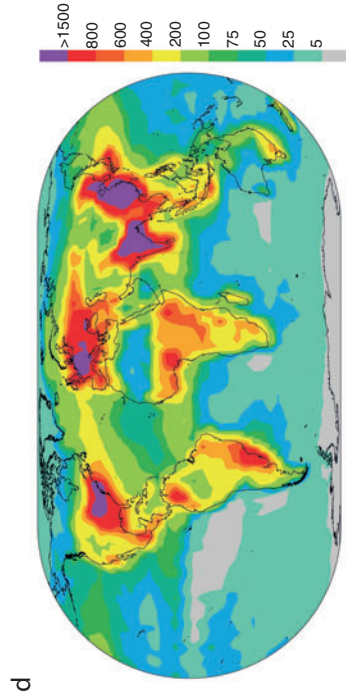
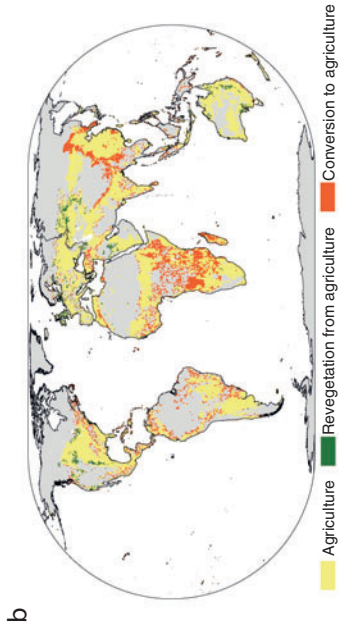
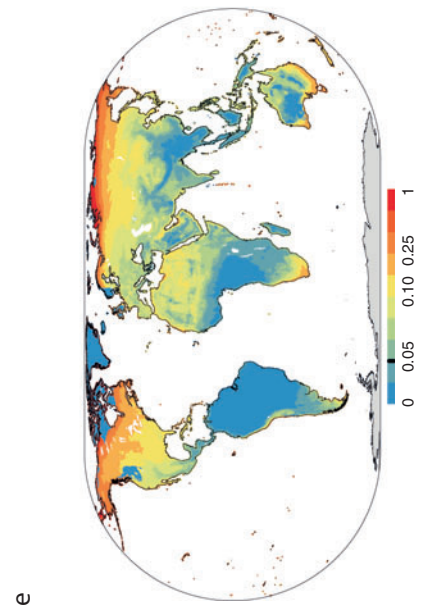
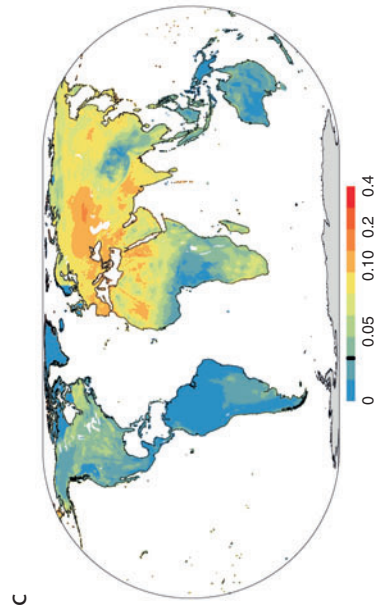
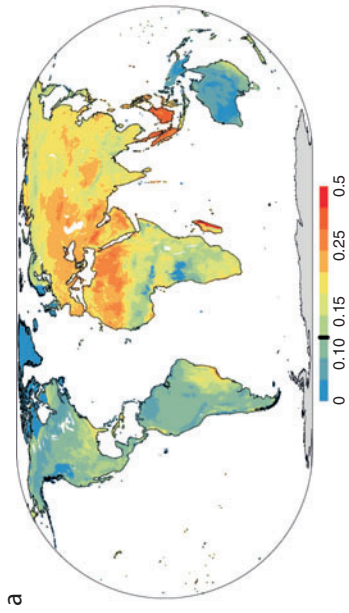


Figure 6

Global distribution of the overlap between terrestrial vertebrate density and incidence (proportion) of threatened species (161, 164). Bright yellow areas have high species richness but low threat; bright blue areas have low species richness but high threat; dark areas have high species richness and high incidence of threatened species; light yellow and light blue areas have low diversity and low threat.



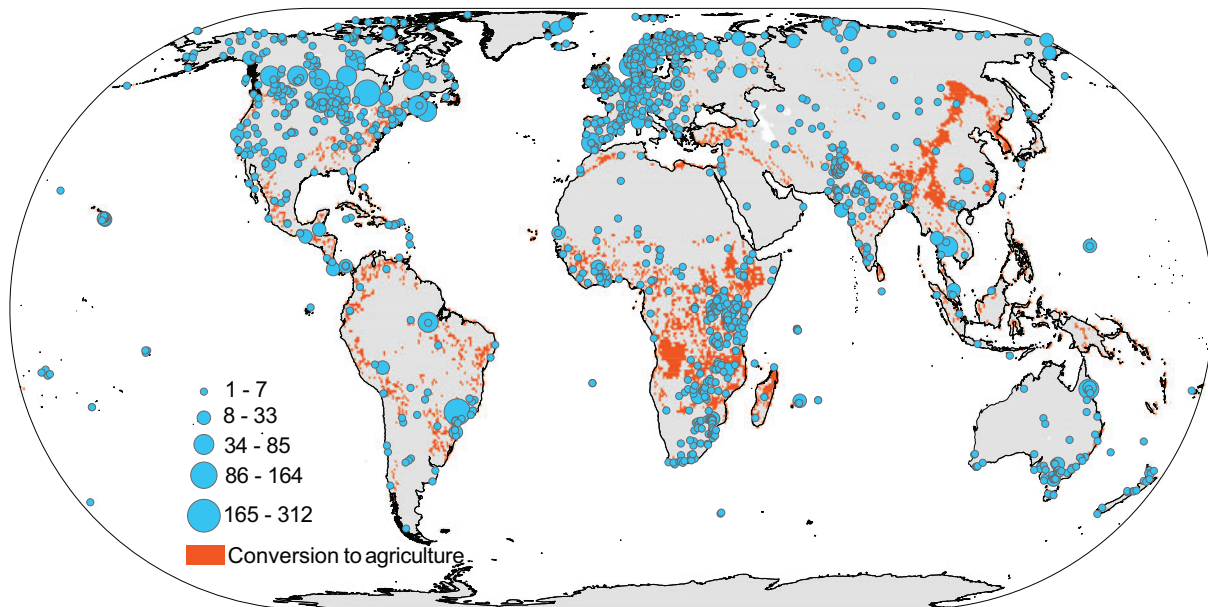


Figure 8

Overlay between the predicted loss of natural habitat and the distribution of the populations monitored by the Living Planet Index (LPI). The circles illustrate the geographical origin of the data used to calculate the annual LPI (20). The size of these points varies according to the number of populations being monitored. The map of land-use change represents the areas of conversion from natural habitat to agriculture, based on the projections of the Order from Strength scenario between 1970 and 2020 (165).

Figure 7

Global distribution of impacts of drivers on terrestrial vertebrates (*panels a,c,e*) and the intensity levels of those drivers (*panels b,d,f*). The impacts include all species listed in the International Union for Conservation of Nature (IUCN) Red List as negatively affected by those drivers, including threatened and nonthreatened species (161). (*a*) Proportion of species suffering from habitat loss (residential and commercial development, agriculture and aquaculture, energy production and mining, transportation and service corridors, and natural system modifications). (*b*) Land-use change between 1970 and 2020: revegetation from agriculture, conversion from natural habitat to agriculture or steady agricultural use. This panel is based on the projections of the Order from Strength scenario (165). (*c*) Proportion of terrestrial vertebrates suffering from pollution. (*d*) Nitrogen deposition (in milligrams of nitrogen/m²/year) in 1993 (166). (*e*) Proportion of species suffering from climate change and severe weather. (*f*) Annual mean surface temperature change between the average of 1965–1975 observations and the average of 2015–2025 model projections for the Intergovernmental Panel on Climate Change B1 scenario (167).