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# Biodiversity: Concepts, Patterns, Trends, and Perspectives

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## Keywords

nature, biological diversity, values, extinction rates, drivers of biodiversity loss

## Abstract

Biodiversity, a term now widely employed in science, policy, and wider society, has a burgeoning associated literature. We synthesize aspects of this literature, focusing on several key concepts, debates, patterns, trends, and drivers. We review the history of the term and the multiple dimensions and values of biodiversity, and we explore what is known and not known about global patterns of biodiversity. We then review changes in biodiversity from early human times to the modern era, examining rates of extinction and direct drivers of biodiversity change and also highlighting some less-well-studied drivers. Finally, we turn attention to the indirect drivers of global biodiversity loss, notably humanity's increasing global consumption footprint, and explore what might be required to reverse the ongoing decline in the fabric of life on Earth.

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## 1. INTRODUCTION

Biodiversity is a charismatic mega-category (1) of our age that is increasingly widely employed in science, policy, and wider society, but means different things to different people. There is no shortage of textbooks and reviews on virtually all aspects of biodiversity. Moreover, there is widespread recognition of the global biodiversity crisis and a United Nations convention dedicated to addressing it. In addition, the past few years have seen an unprecedented number of comprehensive scientific assessments of the state and trends of life on Earth. Three milestones have been the *Global Biodiversity Assessment* (2) in 1995, the Millennium Ecosystem Assessment (3) in 2005, and more recently, the first intergovernmental global assessment, carried out by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (4) in 2019.

In this article, we explore various aspects of and themes in the prolific recent literature on biodiversity. We do not provide an encyclopedic treatment of this vast subject. Rather, we summarize several key aspects, delve into some overarching perspectives on the concept, and also draw attention to points of contention and to emerging themes that have not been sufficiently covered in the literature. Specifically, we focus on the following five themes: (*a*) How did the scientific and policy concept of biodiversity originate and how has its usage evolved over time? (*b*) How and why is biodiversity valued, and what are the tensions and points in different perspectives on the value of biodiversity? (*c*) What have we learned about the nature and pattern of biodiversity on Earth, and how is biodiversity distributed? (*d*) How has biodiversity changed and declined in the human era, from prehistory to modern times? (*e*) What are the direct and indirect drivers of this decline and what might be needed to halt this decline?

**Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES):** an intergovernmental body established in 2012 to strengthen the science-policy interface for biodiversity conservation and sustainable use, and long-term human well-being

## 2. THE CONCEPT OF BIODIVERSITY

### 2.1. The Meaning of Biodiversity Has Changed Over Time, Fast

Today, biodiversity is a widely deployed concept in social narratives, with a prominent presence in the scientific literature, the press, and social media. It is taught in most elementary schools and

is heavily used by the advertising industry. This was not the case 50 years ago. The dramatic rise from obscure technical concept to transdisciplinary boundary object (5) is a vivid illustration of how social practices shape the evolution of scientific concepts.

**Convention on Biological Diversity (CBD):** treaty created in 1992 for biodiversity conservation and sustainable use and fair sharing of the benefits arising from it

The concept of biological diversity can be found in the academic community as early as the mid-twentieth century, with some writers tracing it back to a description of the natural history of the southwestern North American desert by J. Arthur Harris in 1916 (6). It was frequently used in the sense of species number, sometimes accompanied by relative abundance, in a given unit of study, and until the early 1990s most biology graduate students were taught this definition (7, 8). Use of the term biological diversity or its contraction, biodiversity, to encompass biological variability among, but also below and beyond, the level of species first occurred in the 1980s. The first mention of the term biological diversity seems to have been by T.E. Lovejoy in the foreword to a book on conservation biology (9); it rose in prominence in the scientific and science-policy literature in the 1980s, notably through the works of W.G. Rosen, E. Norse, and E.O. Wilson (10), in the context of science-policy initiatives to raise public awareness of the richness of life on Earth and the need to protect it (9). It appeared officially in the intergovernmental science-policy interface in 1992, at the United Nations Conference on Environment and Development (i.e., the Rio Earth Summit), and was formally enshrined into international policy when the United Nations Convention on Biological Diversity (CBD) entered into force in 1993. Article 2 of the CBD defines biological diversity as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems" (**https://www.cbd.int/convention/articles/?a=cbd-02**). Notably, this definition explicitly incorporates ecosystems. Academic definitions up to that point had not included ecosystems probably because ecosystems consist of both living and nonliving components (water, minerals, other physical factors), which by previous definitions could not be part of taxonomic biodiversity. Because of this, many ecologists took (e.g., 11), and still take, exception to this broader definition encompassing variation among ecosystems. Nevertheless, the inclusion of ecosystems in the CBD definition made sense from the policy, legislation, and public communication points of view: Policies and regulations focused on species or communities but that leave out the ecosystems that support them would be difficult to make work in practice. The latest consensus definition of biodiversity in the intergovernmental space, building heavily on that by the CBD, has been established by the IPBES. It reads: "The variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part. This includes variation in *genetic*, *phenotypic*, *phylogenetic*, *and functional attributes*, as well as changes in abundance and distribution over time and space within and among species, biological communities and ecosystems" (**https://ipbes.net/glossary/biodiversity**; italics added). The IPBES definition emphasizes that the focus is on the living components, in an attempt to keep to the spirit of the CBD definition while better aligning it with current ecological theory.

## 2.2. Biodiversity, Nature, and the Fabric of Life on Earth

This rise in usage strongly framed within the science-policy interface explains why the definition of biodiversity has evolved toward increasing inclusiveness (as well as length!) rather than acquiring an increasing sharpness and precision over time. It responds to the need to not only accommodate new facets of life on Earth as their importance is being highlighted by new natural science insights, but also give space to policies, avoid implementation shortcuts, and resonate with the multiple social actors that are increasingly claiming biodiversity as part of their interests and rights. This is a trade-off often experienced by boundary objects (12): wider meaning and social traction versus

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**Anthropocene:** the proposed new geological epoch that marks human domination of key Earth system processes

higher precision and analytical tractability [e.g., a similar tension is seen in the concept of the Anthropocene (13)]. It is clear which path the concept of biodiversity has taken.

In public discourse, and in academic circles too, especially interdisciplinary ones, the word *biodiversity* is now sometimes used interchangeably with two other concepts: *nature* and *the fabric of life*, both of which, although lacking technical precision, appear to resonate better than biodiversity with nonspecialists. *Nature* has the advantage of being simpler and intuitively meaningful to most people without further explanation. To its disadvantage, it carries certain connotations, particularly in recent Western tradition, of untouched wilderness, a concept that many find both inconsistent with the empirical evidence (see Section 5) and socially problematic (14, 15). It also reinforces a sense of the natural world as "other," distinct and separate from humans, which has particular roots in Judeo-Christian and subsequent Enlightenment dualism. This is why some authors prefer to refer to all living entities as the "fabric of life," "woven by natural process over many millions of years and in conjunction with people for many thousands of years" (5, p. 1), in other words, all life around us and within us, with which people are inextricably interwoven (16). This is certainly more convoluted and rather literary, but it provides a vivid metaphor for the deep entanglement of all living entities that multiple social actors find engaging and inspirational.

### 2.3. Biodiversity Is Multidimensional

Whatever the chosen working definition, there is consensus in the literature that biodiversity is multidimensional, encompassing different angles from which to examine and parse the fabric of life: within species (genetic diversity within populations, and across populations of the same species and also of varieties of domesticated plants and animals); across species (taxonomic or organismal diversity at the level of species and higher) within a given area; and across different scales, from local patches to landscapes to biomes and the whole Earth. Diversity at the organismal or community level can be seen from the perspective of taxonomy (e.g., 8), phylogeny (e.g., 17), or functional traits (e.g., 18), and within each of these facets and perspectives, one can focus on the richness of entities or components present, the distribution of abundance among these entities (evenness or its counterpart, dominance, measured as number of individuals, biomass, or productivity), or the identity of particular entities (composition). There is a vast literature on the basics of these concepts and on the myriad metrics designed to capture them, and we do not attempt to cover them here. There is no simple best facet or metric to convey the state and trends of biodiversity; there is a trade-off between simplicity (and thus feasibility of having long-term standard records worldwide) and functional meaning, and none of these metrics captures the full value of biodiversity to people.

## 3. THE DIVERSE VALUES OF BIODIVERSITY

Not only is biodiversity multidimensional, it also encompasses diverse values; that is, different people attribute different meanings and levels of importance to it. A major distinction arises from holding predominantly biocentric or anthropocentric worldviews. Biocentric worldviews favor intrinsic values, which are those of nonhuman nature per se, irrespective of any human consideration. By contrast, anthropocentric worldviews favor human-focused values. For example, the notion of nature's contributions to people—the myriad positive and negative effects that different components of nature, or nature as a whole, have on people as individuals, societies, or the whole of humankind (19)—is anthropocentric. Anthropocentric values of nature and its contributions to people range from strongly instrumental (i.e., the value of organisms, genes, ecosystems, landscapes as a means to achieve specific human ends) to strongly relational (i.e., values that do not directly emanate from nature but are derivative of our relationships with it and our responsibilities



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toward it, and that are involved in the ideas of a meaningful and fulfilling life and the "right thing to do") (20–22). Entities of nature to which one ascribes instrumental value are often replaceable by other entities that serve equally well toward a certain human end. In contrast, entities to which one ascribes relational value are often irreplaceable. For example, a cherry tree in your front yard can have intrinsic value, associated with the right of the species or that particular tree to exist, independent of its usefulness or importance to you or anyone else. The tree can also have several instrumental values, such as providing cool shade, edible fruit, aesthetically pleasant flowers, food for pollinators, and structure for urban avifauna, which in turn are a source of enjoyment and inspiration. Some of these values can be expressed in monetary terms, such as the worth of the wood or the cherries. Some of these values are commensurable; that is, they can be meaningfully expressed using the same metric, such as money or biomass. But even if these values were incommensurable (i.e., they are not comparable on a common scale) in terms of the benefits the tree provides, the cherry tree is fully replaceable by another cherry tree similar in health, stature, and age. And if the tree also produces detriments (e.g., it attracts bees to which you are allergic, obstructs circulation, or seriously annoys the neighbors), a trade-off analysis of benefits versus detriments can be made, and a decision can be reached on whether the tree is worth keeping or cutting. But if this cherry tree was planted for you by your mother when you were a child, it acquires a relational value well beyond any of these instrumental benefits, a value that even outweighs any instrumental detriments it may produce. It is "your" cherry tree and thus cannot be replaced with a similar cherry tree.

Intrinsic or biocentric values have long been highlighted by nature lovers and conservationists. Our modern scientific geobiosphere consensus, which recognizes the biosphere as varied and evolving for vast eons of Earth's history prior to very recent human evolution, and in which there is no inevitability to human emergence, also resounds with a deeply biocentric worldview. Instrumental values of nature have been receiving increased attention since the early 2000s, such as from various initiatives focused on ecosystem services (23, 24). The notion of relational values, in contrast, has been largely neglected in the literature until recently, even though these values are some of the strongest and most common motivations in people's struggles to protect species, ecosystems, or even venerable individual organisms (21, 25).

In practice, different kinds of values frequently intermix in underpinning people's decisions about nature, and it is probably of little practical importance to establish a sharp distinction between them in particular cases. Importantly, no one kind of value is more important than another, no single metric would do justice to all that people find important about nature, and many different values come into play in decisions about a particular aspect of nature (22). Even more important, the same entity can encompass vastly different values (on a different or on the same scale) for different people; there is no single objective answer for how much an entity of nature is worth. Therefore, it is crucial that discussions on value be pluralistic, in terms of both the multiple dimensions of value and the social actors involved. The discussion of how to best value nature, until recently dominated by technical issues (e.g., the need for better precision and standardization), is now increasingly focused on issues of equity, legitimacy, and inclusiveness (e.g., who gets to decide the value of nature, from which perspective, and who benefits from and who is damaged by the final decision). In other words, social valuation for decision-making is now increasingly seen as an arena for deliberation and social negotiation, as well as a technical issue (15, 20, 26–28).

## 4. THE PATTERNS OF BIODIVERSITY

We next briefly review how biodiversity, in terms of phylogenetic structure and geography, is distributed among life on Earth. We explore why such patterns exist and what drives exceptionally



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high levels of diversity in some groups and regions. We summarize recent estimates of the total amount of biodiversity on Earth, how these estimates arise, and what the key uncertainties are. We touch upon the complexities in definition and scaling, with a particular focus on prokaryotic diversity, which is probably the least understood component of biodiversity.

## 4.1. How Much Biodiversity Is There?

At the higher levels of the taxonomic hierarchy, the tapestry of life can be partitioned into several kingdoms. The number of such kingdoms has increased as our understanding of the deep taxonomy of life has improved; the most recent broadly adopted approach proposes seven kingdoms of life (29, 30), divided between a prokaryotic superkingdom consisting of bacteria and archaea and a eukaryotic superkingdom consisting of protists, chromists, fungi, plants, and animals (**Table 1**). The protists and chromists are considered polyphyletic (i.e., consisting of many inconsistently connected clades), and all other eukaryotes evolved from the protists.

Life on Earth can be quantified in many different ways. Three major approaches are to estimate the number of species, the amount of evolutionary history, or the amount of biomass. The most widely employed approach is to estimate species number. There are approximately 2 million eukaryotic species on Earth (**https://www.catalogueoflife.org/**), of which approximately one-half are insects and approximately one-fifth are vascular plants (mostly flowering plants). The remaining eukaryotes are an assorted variety of life forms, dominated by fungi (approximately 7%), with all vertebrates representing only approximately 4% of the total known species (31–33). Note that these figures refer to species already described; there is high uncertainty about how many species there are in total. The most widely cited assessment uses the relationship between taxonomic level and species diversity of better-understood taxonomic groups to infer species counts for more poorly understood groups (34) (**Figure 1**; **Table 2**). This approach suggests 8.7 million eukaryotic species (±1.3 million). Approximately 8.1 million of these are plants and animals, of which approximately 5.5 million are insects (34, 35). We are nowhere near describing

**Table 1 Estimated total number of species on Earth in the seven kingdoms of life (29, 30)**

| (Super)Kingdom | When evolved | Structure | Number of species (total) | Number of species (marine) | Number of species (terrestrial) |
|---|---|---|---|---|---|
| **Superkingdom Prokaryota** | | | | | |
| Bacteria | 3–4 Gyr | Unicellular | 1,250,000 (0.8–1.7 million) | NA | NA |
| Archaea | 3–4 Gyr | Unicellular | 105,000 (70,000–140,000) | NA | NA |
| **Superkingdom Eukaryota** | | | | | |
| Protozoa | 1.5 Gyr | Unicellular | 36,400 | 36,400 | 0 |
| Chromista | 1.2 Gyr | Unicellular | 27,500 | 7,400 | 20,100 |
| Fungi | 1 Gyr | Unicellular or multicellular | 611,000 | 5,320 | 605,680 |
| Animalia | 700 Myr | Multicellular | 7,770,000 | 2,150,000 | 5,620,000 |
| Plantae | 500 Myr | Multicellular | 298,000 | 16,000 | 281,400 |
| **Total species** | | | **10,100,000** | **2,210,000** | **6,540,000** |

Estimates for eukaryotic species are from Reference 34; estimates for prokaryotic species (operation taxonomic units) are based on Global Prokaryotic Census (39). Total marine and terrestrial species estimates are for eukaryotes only (34). Species numbers for protozoa are very likely to be largely underestimated.

Abbreviation: NA, not applicable.



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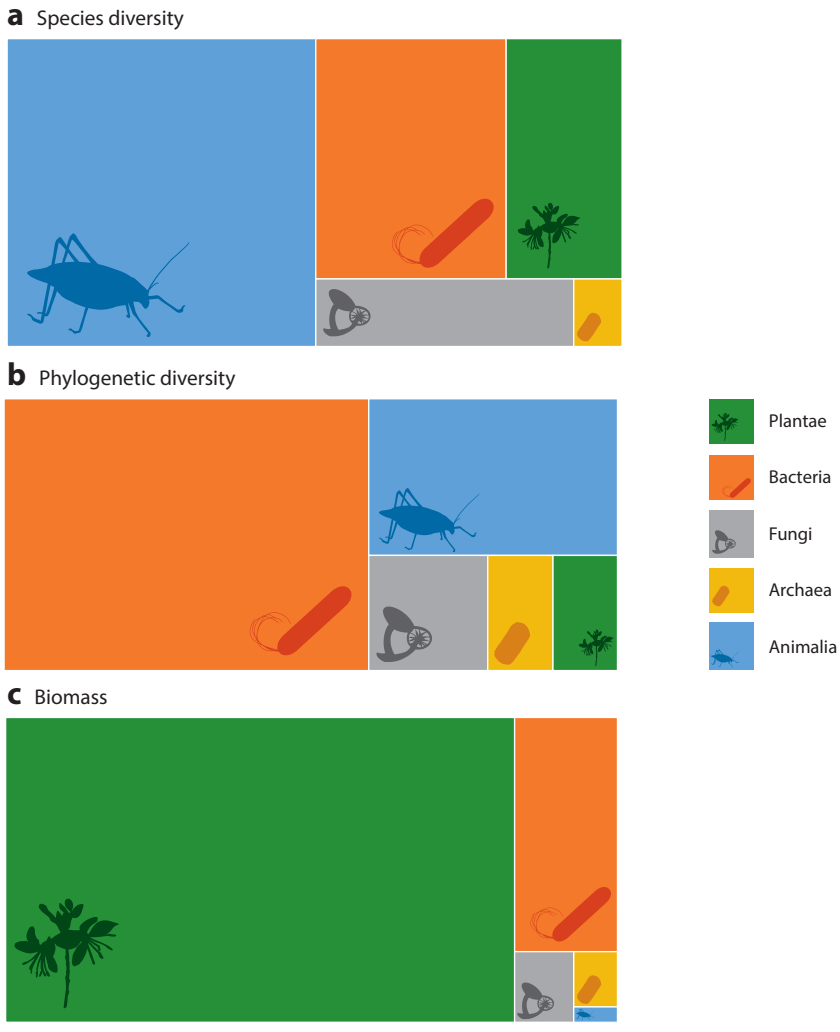



**Figure 1**

Distribution of global biodiversity in the major kingdoms of life through the metrics of (*a*) species diversity, (*b*) phylogenetic diversity, and (*c*) biomass.

all species on Earth: According to the same assessment (34), and assuming that the average effort and cost to describe an animal species remain constant (this could change dramatically with new technology, for example), it would take approximately 1,200 years and the effort of 303,000 taxonomists to describe all eukaryotic species on the planet. Recent estimates (36) employing molecular-based species delimitation (rather than the usual morphology-based delimitation) of arthropod species boundaries controversially suggest that eukaryotic diversity may still be much higher (approaching 1 billion species in total).

The two prokaryotic kingdoms, Bacteria and Archaea, are the most ancient and widespread manifestations of life on Earth, are found in every ecosystem, and drive most global biogeochemical cycles. They present even more challenges in both defining species and quantifying species diversity. Formal description of a microbial species would usually require isolating it in



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**Table 2 Quantifying life on Earth through different metrics**

| Taxon | Biomass (Pg C) | No. of species/OTUs | Estimated phylogenetic diversity (billions of years) |
|---|---|---|---|
| Plantae | 450 (1.2×) | 419,300 | 15,384 |
| Bacteria | 70 (10×) | 690,474 | 205,419 |
| Fungi | 12 (3×) | 261,800 | 28,330 |
| Archaea | 7 (13×) | 49,406 | 15,531 |
| Animalia | 2 (5×) | 1,429,766 | 80,703 |
| Arthropods | 1 | 1,152,722 | 43,028 |
| Fish | 0.7 | 35,810 | 1,512 |
| Mollusks | 0.2 | 89,359 | 4,233 |
| Cnidarians | 0.1 | 14,566 | 896 |
| Nematodes | 0.02 | 18,509 | 1,023 |
| Mammals | 0.007 | 5,045 | 66 |
| Birds | 0.002 | 9,993 | 81 |
| Humans | 0.06 | 1 | 0.01 |

Eukaryotic species numbers refer to species cataloged on the Open Tree of Life (**https://opentreeoflife.github.io/**), accessed in December 2021; prokaryotic species numbers (OTUs) are from the Global Prokaryotic Census (39). Numbers refer to described species (eukaryotes) or quantified OTUs (prokaryotes). Evolutionary history was estimated as Faith's PD (44) by James Rosindell (personal communication); these are rough estimates with rounded decimals and in some cases were extrapolated from only species richness and clade age assuming a log-linear growth of lineages over time, based on the Open Tree of Life and Reference 196. Biomass numbers are from Reference 45, with numbers in parentheses indicating the multiplicative range of uncertainty.

Abbreviations: OTU, operational taxonomic unit; PD, phylogenetic diversity.

pure culture and describing it biochemically and morphologically. However, only approximately 1% of prokaryotic species can be isolated in culture with current techniques (37). Moreover, the concept of species boundaries is particularly challenging for quantifying prokaryotes because the widespread occurrence of lateral transfer of DNA between lineages complicates the definition of species. Lateral transfer has led researchers to suggest that prokaryotic cells are simply holding vessels for a single prokaryotic metaspecies gene pool, with the part of this pool seen in any single cluster (species) simply being the genes that are selectively useful in a given environment (38). However, this is not the prevalent view and it is recognized that most gene transfer occurs between prokaryotes of similar genetic composition, where the lateral gene transfer within groups is much greater than the transfer across groups, enabling phylogenetic history to be preserved when genomes are compared. A practical definition is to consider operational taxonomic units (OTUs), where typically 97% of genetic material is shared, with the 16S rRNA gene used as a point of comparison (39). Total prokaryotic diversity is a subject of controversy, constrained by both limited sampling and questions of appropriate scaling. Some authors have suggested that prokaryotic diversity may reach up to a trillion ($10^{12}$) species (40) based on extrapolating empirical scaling laws of local diversity in individual communities to global scales. This view would imply that prokaryotes are the overwhelming dominant component of terrestrial diversity.

The Global Prokaryotic Census compiled sequencing data from 2,800 locations to estimate prokaryotic diversity (39). These samples were taken from the vast environments in which prokaryotes are found, including surface- and deep-ocean water, oxygen minimum zones, freshwater and hypersaline lakes, rivers, groundwater, marine surface and deep subsurface sediments, agricultural and forest soils, peats, permafrost, deserts, animal guts and feces, plant leaves and rhizospheres, salt marshes, bioreactors, processed food, methane seeps, mine drainages, sewages,



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hydrothermal vents, and hot springs. The census identified approximately 740,000 prokaryotic OTUs, of which approximately 90% were bacterial (**Table 2**). It then employed statistical scaling methods to estimate total prokaryotic diversity, arriving at 0.8–1.7 million OTUs for bacteria and 70,000–140,000 OTUs for archaea (**Table 1**), large numbers but at the low end of some of the previous estimates described above. A key source of uncertainty is the extent of geographical variability and also of host-taxon-specific variability in microbiomes (41, 42); if microbiome diversity is specific to the host taxon, total prokaryotic diversity could be much higher. The evidence to date suggests that taxon-specific microbiomes show only modest variation across related host taxa and that biogeographical variation is even lower, with the same prokaryotic species found in the same environments worldwide. Among the eukaryotes, protist diversity has a set of challenges similar to that for prokaryotic biodiversity and is also probably greatly underestimated, with soils being a particularly rich habitat (43).

**Deep biosphere:** the part of the biosphere that resides below the first few meters of the land and seafloor surface (the zone of animal bioturbation)

A second approach is to estimate how much evolutionary history, or how much of the Tree of Life, is embodied in a set of taxa. One of the most used metrics is phylogenetic diversity (44), which is the summation of the branch lengths connecting a set of taxa on a phylogeny. Although it gives different information than species diversity, phylogenetic diversity is broadly correlated with species number within specific taxa, because additional species add at least one extra branch to the tree, but it also reflects the taxonomic depth of clades. In terms of phylogenetic diversity, our planet appears dominated by bacterial phylogenetic diversity, which underpins the diversity of metabolic toolkits that life has developed over its deep evolutionary history (**Figure 1**; **Table 2**).

A third approach is to estimate Earth's total living biomass. This task is far from trivial, especially when soil and sediment ecosystems are considered, particularly the deep biosphere of bacteria and archaea living in the planetary crust. Bar-On and colleagues (45) undertook a heroic assessment and synthesis of hundreds of studies (**Figure 1**; **Table 2**). They estimated the total biomass of life to be 550 Pg C (95% CI 323–935 Pg C). This estimate is in carbon units, roughly equivalent to 1,100 Pg of dry biomass or approximately 1,800 Pg of naturally hydrated biomass. Plants dominate this estimate at 450 Pg C (375–540 Pg C); however, global plant biomass is 70% woody tissue, which is relatively (but not totally) metabolically inert. Hence, the more metabolically active component of plant matter (primarily leaves, fine roots, green stems, flowers, and fruit) sums to approximately 135 Pg C, still about twice that of the bacteria, which place second in this biomass ranking at 70 Pg C, though with a large uncertainty (7–700 Pg C). Ninety percent of bacterial biomass occurs in the deep surface (mainly in aquifers and below the seafloor) and also has slow metabolic activity. Hence, in terms of metabolic activity and energy flow, plants almost certainly dominate life on Earth. While animals dominate the species diversity metrics, they account for only 2 (0.4–10) Pg C of biomass, approximately 0.4% of the total.

In summary, according to the metric applied, different kingdoms of life rise to prominence, with plants dominating in terms of biomass and metabolic activity, animals in terms of known species diversity, and bacteria in terms of phylogenetic diversity and diversity of metabolic innovations (**Figure 1**; **Table 2**).

## 4.2. Causes of the Geographical Patterns of Biodiversity

Approximately 90% of known species diversity is found on land, primarily because insects are predominantly a terrestrial clade, but the prevalence of terrestrial species persists even without counting arthropods. Land environments tend to incorporate a wider range of environmental heterogeneity (e.g., wider range of microclimates and microenvironmental conditions; varying levels of restrictions in water supply; less easy lateral mixing than, for example, through ocean currents).

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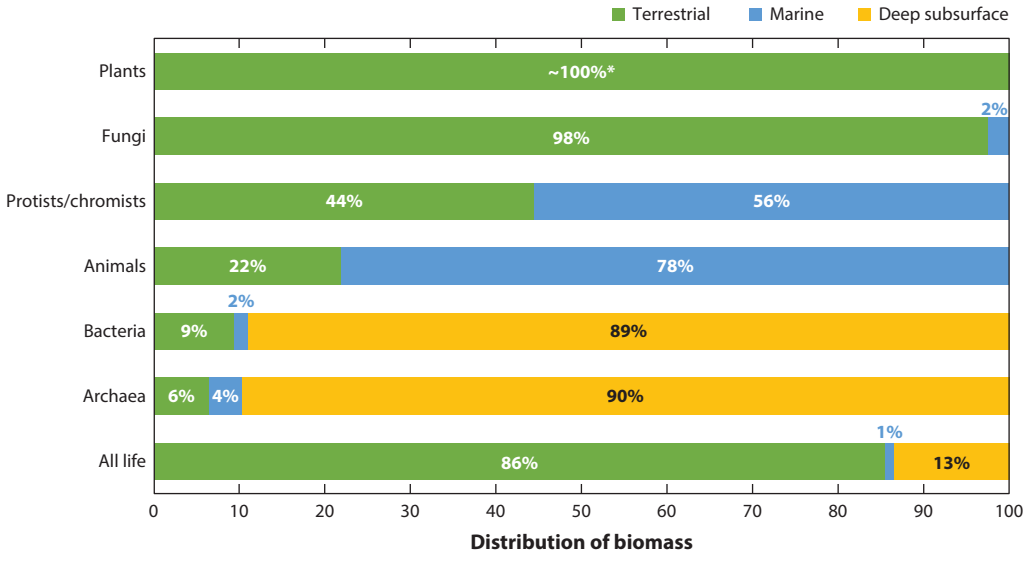



**Figure 2**

The distribution of biomass between terrestrial (*green*), marine (*blue*), and deep subsurface (*yellow*) environments in the main kingdoms of life. Derived from Reference 45. The asterisk corresponds to land plants, which represent more than 99.5% of the total plant biomass (46–48).

However, as the point of origin of life on Earth, the oceans contain a higher level of deeper taxonomic diversity, with many phyla present that have not made a transition to land environments (e.g., cnidarians, sponges, echinoderms).

The biomass of life is also predominantly terrestrial, as plants are dominant organisms that shape terrestrial environments and, in the case of trees, have evolved long-lived woody forms that enable high biomass to be created and maintained. Marine ecosystems have similar global primary productivity to that of terrestrial ecosystems (90 Pg C $year^{-1}$ for marine systems compared with 120 Pg C $year^{-1}$ for terrestrial ones), but because phytoplankton are single celled and short lived, marine biomass accounts for a small fraction of planetary biomass and is more concentrated at higher trophic levels (**Figure 2**). Meanwhile, the poorly described deep subsurface biosphere accounts for the vast amounts of bacterial and archaeal biomass, although its species/OTU diversity is still poorly understood (**Figure 2**).

This pattern of domination of global species-level diversity by land biota seems relatively recent, associated with the rise of the (overwhelmingly terrestrial) angiosperm plants approximately 100 million years ago and with the diversification by arthropods as specialist mutualists or predators (49), although issues around preservation bias toward more recent times cast an element of uncertainty around past projections of biodiversity trends.

Ultimately, in terms of number of species, the extant number of species is the end product of historical rates of speciation and extinction. A biome can facilitate high rates of speciation through provision of microenvironmental niches or isolation; enhanced biotic pressures through competition, predation, parasitism, or pathogens; enhanced biotic synergies and mutualisms; higher rates of generation turnover; or higher rates of mutation. Biomes may also facilitate high rates of extinction through environmental variation over time, disturbance regimes, and strong abiotic filters (e.g., climate) that limit the potential for new species to be successful. Past environmental change also plays a major role in shaping modern biodiversity. For example, the temperate forests of Europe are much less diverse than those of East Asia because these ecosystems (including



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soils) have assembled from isolated glacial refugia into postglacial environments only in the last 11,000 years, whereas East Asia avoided extensive glaciation (50). Similarly, the tropical forests of Africa appear less diverse in plants than those of Asia and the Americas, a pattern that can be explained by a higher level of past extinctions driven by climate variability in Africa and also by elevated rates of speciation associated with tectonic activity in Asia and the Americas (51).

Hence, species-rich biomes can be cradles of biodiversity (high speciation rates), museums of biodiversity (low extinction rates), or both. Recent phylogenetic, geomorphological, and modeling analyses are shedding new light on species-rich regions. A good example is the Amazon tropical rainforest, the most species-rich biome on Earth. This region appears to be both a cradle and a museum. The lineage diversity of the Amazonian biota is quite old, with many plant families dating back to (or before) the emergence of angiosperm-dominated tropical rainforests approximately 65 million years ago. However, most Amazonian species are young, dating from the Pleistocene (last 2.6 million years) (52). The Andes mountains and their complex topography and microenvironments are unique in that they compose a long north-south mountain chain adjacent to a tropical rainforest. Their complex topography, coupled with climate variability, appears to have been pivotal in providing microenvironments that facilitate high levels of speciation, refugia that reduce the rate of extinction, and migration corridors that facilitate species adaptation to climate change (53). The interaction between cradle and museum roles can be spatially complex. For example, for birds in the Americas it appears that low-diversity and environmentally stressful environments such as temperate or montane regions act as centers of speciation, whereas subsequent spread of species results in low-stress lowland tropical regions being museums of biodiversity (54).

## 5. HUMANS AND TRENDS IN BIODIVERSITY

### 5.1. Humans and Biodiversity Change in Premodern Times

Being social megafaunal omnivorous predators and competitors, species of the genus *Homo* are likely to have always affected the biodiversity of ecosystems they have inhabited. Indeed, its ability to construct a wide array of environmental niches (55, 56) is a key attribute of *Homo*. Human shaping of the biota started in the Pleistocene through hunting, transport of other species, and the use of fire (55, 57–59), and by the start of the Holocene, approximately 12,000 years ago, roughly three-quarters of terrestrial ecosystems were already inhabited by people (60). There is evidence that some species extinction associated with the emergence of *Homo erectus*, with its larger brain size, associated shift to a more heavily meat-based diet, and use of fire as a strategy to modify ecosystems and cook foodstuffs, may have taken place in Africa 1–2 million years ago (61). The more striking evidence emerges from the megafaunal extinctions that are loosely associated with the spread of *Homo sapiens* out of Africa and across continents and islands. Vertebrate megafauna (>44 kg mass) appeared particularly vulnerable on continents because of their slow generation times and large range requirements (58). The role of humans in Pleistocene megafaunal extinctions remains debated, partially because in any one locale it can be hard to definitively separate the poor archaeological record of human presence from other possible environmental factors. However, when the global picture is considered, it is hard to deny that human arrival is associated with the loss of many species, possibly in some cases in association with climate variation that put short-term pressure on megafaunal populations (62–64). This argument is reinforced when we consider that climate has fluctuated from glacial to interglacial conditions throughout the Pleistocene without causing extensive megafaunal extinction. In total, 178 megafaunal mammals are thought to have gone extinct in the Late Pleistocene Extinctions (64). Across continents, it is estimated that Eurasia has lost 9 of 28 megafauna species; Australia, 14 of 16; North America, 50 of 60; and South America, 34 of 47. Africa was the least affected continent, and it

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is interesting to speculate why (65). The most frequent argument is that species there (and to a lesser extent southern Eurasia) coevolved with hominids and learned to fear their potential as predators, whereas species in other continents were ecologically naive to the threat these puny primates presented. However, several megafauna species (e.g., proboscideans) show high behavioral and social intelligence and could be expected to learn rapidly in response to new threats. An alternative or complementary argument is that Africa experienced a long, drawn-out megafaunal decline under successive waves of hominids over the 2 million years of the Pleistocene. A recent study from the southern Levant shows a steady decline of large-mammal biomass throughout the Pleistocene across occupation by *Homo erectus*, *Homo neanderthalensis*, and *Homo sapiens*. By 10,500 years ago, the average biomass of mammal remains was only 1.5% of that found 1.5 million years ago (66). The impacts of these extensions likely extended beyond the species themselves, as large animals play key roles in shaping ecosystem structure and functions such as nutrient cycling (67, 68).

In the Holocene, the pattern of species loss continued on island systems (including large islands such as Madagascar and Aotearoa/New Zealand), spreading through a much wider range of body mass. Endemic island faunas appear particularly vulnerable because of their depauperate environment, ecological naivety, and lack of resistance to human-associated species such as rats. The Polynesian expansion across the Pacific is associated with the extinction of approximately 1,000 endemic bird species (mainly flightless rails); this is almost certainly the largest vertebrate species extinction event of the Holocene thus far (69).

This history of global extinctions since the Pleistocene, and the modern trends described in the next section, may lead to the conclusion that human impacts on biodiversity are negative by definition. While the global balance is overwhelmingly negative, and megafauna and island endemics are particularly sensitive, human activities have also deliberately or involuntarily fostered biodiversity throughout history, including to the present day. This can happen in several ways. After the extinction event associated with the first arrival of humans in exotic ecosystems, many Indigenous cultures developed systems of reciprocity and stewardship based on a close understanding of local ecosystems. In its simplest form, disturbance associated with human activities, especially at low to medium intensities and small spatial scales, creates habitat heterogeneity (70) and prevents competitive dominance, favoring the coexistence of a higher number of species at the level of both local patches and whole landscapes. At the other end, many ancient and elaborate farming or stewardship practices and institutions by Indigenous peoples and local communities around the world have deliberately fostered particular organisms, biotic assemblages, or whole ecosystems (33, 71–73). Some of the meadows and grasslands with the highest richness of vascular plants are in long-managed landscapes in Europe, maintained by extensive traditional management by local communities over hundreds or thousands of years, in areas that otherwise would be much more homogeneously dominated by coniferous or broad-leaved shrubs or forests (70, 74). In many regions, there is evidence of ancient gardening for useful wild plants, contributing to their dominance. Complex cultural landscapes combining wild and domesticated plants and animals are still maintained today around the world, including traditionally burned hunting and grazing lands in Africa and Australia; complex agricultural mosaics in the Pacific Islands (75); *dehesas* (savannah-like landscapes) in southern Europe; hay and sheep grasslands in Europe and Asia; forest gardens in tropical Asia, Africa and Latin America; *vegas* (wet meadows) in the high Andes; and *satoyama* landscapes (a mosaic of forests, rice fields, grasslands, streams, and irrigation infrastructure) in Japan (33). While the main focus of these practices tends to be on a small number of species, these gardened patches often favor other wild organisms at all trophic levels, such as bees and other insects, frugivorous mammals and birds, and fungi, that are rarer in either more intact or more industrially managed areas.



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The examples above mostly involve favoring organisms that already exist in a region, although in fewer places and/or at lower densities. Another key way people have fostered diversity in the broadest sense is by creating, predominantly by deliberate selection based on initially wild species (76), a large number of domesticated plant, animal, and microbial phenotypes (e.g., livestock, poultry, work and ornamental animals, food, fiber and fuel crops, ornamental plants, yeasts, fungi). Although small compared with the whole of wild genetic diversity on Earth, domesticated diversity is far from being insignificant. The total number of domesticated phenotypes (variously termed varieties, land races, breeds, or strains depending on the organism and sector; hereafter termed varieties) is unknown beyond particular groups. However, a rough estimation of well-monitored domesticated terrestrial animals and plants that contribute to major food groups is approximately 300 species (77). This number is dwarfed by the number of derived varieties: almost 1 million, dominated by grains, tubers, and legumes (77). A stocktaking restricted to terrestrial farm mammals and birds, excluding those believed to be extinct, yielded 8,179 in 2016 (78). The numbers are bound to be much higher when considering aquatic animals, ornamental and companionship animals, ornamental plants, and microorganisms. The social, cultural, and economic importance of domesticated biodiversity to humanity is immense (33, 77–79).

## 5.2. Modern Biodiversity Decline

The rate of decline of biodiversity has intensified in modern times. Several defining features of the model of human appropriation of nature that is globally dominant today were already present in premodern times. However, the scale increased dramatically, coinciding with step changes in globalization and economic mercantilism (80): the onset of the European exploitation of the Americas and other colonized regions at the turn of the sixteenth century, the Industrial Revolution in the late eighteenth and early nineteenth centuries, and the Great Acceleration (81) since the 1950s. As a consequence, the extent and integrity of natural ecosystems, the distinctiveness of local communities, the size and geographical spread of plant and animal populations, the number of species, and the intraspecific genetic diversity of wild and domesticated organisms have all decreased (5, 33). These declines have been accompanied by two other global processes that have received less public attention. The first process, termed biotic homogenization, consists of a decrease in the taxonomic, functional, phylogenetic, and species-richness distinctiveness of regional biotas across the world due to deliberate or involuntary transport of organisms by humans (82, 83); such a degree of reshaping of global biogeography was termed a New Pangaea by Harold A. Mooney (84). For example, in the past five centuries, there has been a widespread homogenization of plant communities, but this is much more the result of species becoming naturalized beyond their native ranges than of the extinction of native species (85).

The second widespread process is contemporary evolution, that is, the ongoing or recent heritable phenotypic changes taking place in wild populations (86, 87) as a consequence of directional selection pressures by humans such as hunting, fishing, urbanization, use of agricultural biocides, or development of transport or irrigation infrastructure. These pressures are mostly unintended in the sense that the phenotypic changes are a collateral effect rather than a desired target of the activity, as opposed to, for example, selective breeding. The number of examples has escalated in the past few years (33, 88, 89), probably because of a shift in attention rather than an acceleration of contemporary evolution per se. The worldwide reconfiguring of life on Earth at all levels, from genes to biomes, by humans has prompted rich discussions in ecological, philosophical, and policy arenas (5, 15, 80, 90, 91).

We next focus particular attention on wild species extinctions and trends in taxonomic and functional composition of local communities, as they are areas with abundant data worldwide, standardized and widely adopted methods, and a rapidly growing literature.



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**5.2.1. Extinction risks and rates.** That our planet is quickly losing species is well known to scientists and is one aspect of nature's decline best known by the wider public. Because of this, a stocktaking of the status of biodiversity at the species level must include not only the number of species and higher-order taxa, their geographical distribution, and their abundance, but also their risk of disappearing at human-relevant timescales. Three kinds of extinctions at the species level are relevant. While catastrophic extinction events that suddenly extirpate a species from the face of the Earth do occur, most extinctions occur more or less gradually. They start when species become increasingly rare in some locations and, while their populations are still high enough to persist in the long term, they are too small to fully perform some of the species' ecological roles; this is called functional extinction (92). The second kind is local extinction, which is when a species goes extinct in part of its range but persists in other areas. For example, lion (*Panthera leo*), guanaco (*Lama guanicoe*), and bison (*Bison bison*) today occupy a small fraction of their former distributional range. Finally, a species is said to be globally extinct when it disappears from the Earth. While the first two kinds are undoubtedly important, most of the global monitoring efforts and thus most of the published information deal with global extinctions, which we discuss in the rest of this section. The two most common ways to refer to global extinctions are extinction risk and extinction rate. These complementary metrics provide different insights into the extinction process.

Extinction risk indicates how likely a species will go extinct. It is established for clearly identified species, typically before they disappear, and it considers the species biology and the external threats a species faces. The system most used to categorize extinction risk is that carried out by the International Union for Conservation of Nature (IUCN). The IUCN uses a set of standardized categories (the IUCN Red List categories; **https://www.iucnredlist.org/**), ranging from least concern (not in need of specific conservation efforts) to critically endangered (50% chance of going extinct in the next 10 years), for species still found in the wild, plus two categories of extinct species (extinct and extinct in the wild). Threatened species (vulnerable, endangered, and critically endangered) are those species judged to be at high extinction risk at present.

Extinction rates, on the other hand, indicate the speed at which taxa disappear over a time period. Estimation of these rates is often carried out a posteriori (when species have already disappeared) and usually does not refer to specific species but rather to large groups of species or whole biotas. Rates are often expressed in number of extinctions per million species per year (E/MSY) to standardize comparisons among different time periods and sets of species. These extinction rates are often compared with the background rate, that is, the average extinction rate due to nonhuman causes over geological history. The present consensus for the background rate of extinction is approximately 1 E/MSY, although there have been arguments for substantially higher (93) or lower (94) rates (**Figure 3**). For easier comparison with rates at present and in the near future, 1 E/MSY is equivalent to 1 species extinct in a total sample pool of 10,000 species over a time period of 100 years (95).

According to the most comprehensive review to date, the total number of animal and plant species—both known and unknown to science—now threatened with extinction is estimated to be 1 million (5, 33). This risk estimation is based, on the one hand, on the estimated total number of plant and animal species on Earth (8.1 million, of which 5.5 million are insects (34, 35); see above) and, on the other hand, on the proportion of threatened species in different major groups of organisms according to the IUCN Red List. This proportion is not equally well known for every group. For example, legumes, ferns and allies, monocots, mammals, birds, and reptiles have been comprehensively assessed, whereas in other groups, such as fish and invertebrates (including some mollusks, insects, crustaceans, and corals), only representative samples have been assessed. And even among the comprehensively assessed, there are not enough data to assign a risk category to many species; the percentage of data-deficient species varies widely, for example, from 0.4% in



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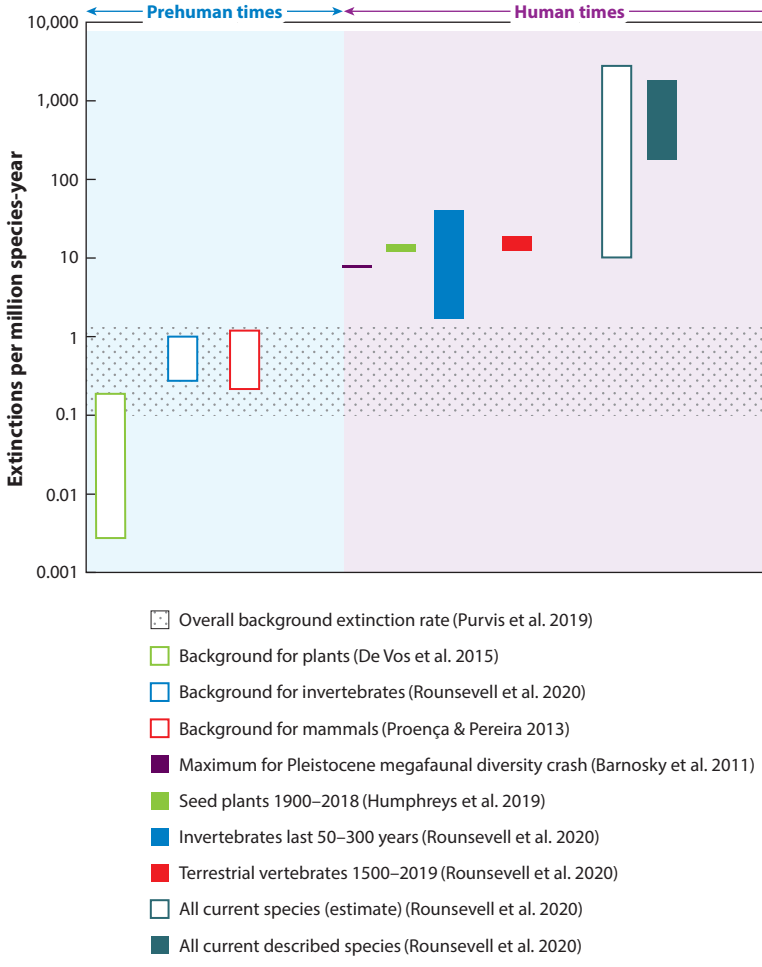



**Figure 3**

How present extinction rates compare with those of the past. Extinction rate estimations by different authors vary widely depending on taxa, timespan, and methods considered, but modern extinction rates greatly exceed those in prehuman times. Figure adapted with permission from Reference 100. Data for the overall background extinction rate are from Reference 33, based on References 93, 94, 98, 101; the background and present extinction rates for plants, from References 94 and 97, respectively; the background extinction rate for invertebrates, from Reference 100 (fossil insects); the background extinction rate for mammals, from Reference 95, based on References 98 and 102; the maximum extinction rate for the Pleistocene megafaunal diversity crash, from Reference 98; the extinction rate for seed plants from 1900 to 2018, from Reference 97; the extinction rate for invertebrates for the last 50–300 years, for terrestrial vertebrates from 1500 to 2019, for all current species (estimate), and for all current described species, from Reference 100.

cycads to 40% or more in some invertebrates. Acknowledging all these uncertainties, the average proportion of threatened species (all categories, from vulnerable to critically endangered) across all assessed groups of animals, plants, and noninsect invertebrates is approximately 25%. The risk for insects as a whole is largely unknown. For Odonata (dragonflies), the only globally assessed group, approximately 15% are threatened, but the fact that freshwater habitats face many threats may mean that other insects have lower levels of extinction risk. Assessments of several insect groups

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(bees, butterflies, saproxylic beetles) in Europe have assigned a risk prevalence closer to 10%. On this basis, 10% was used as a conservative proxy figure for insects—the true value might be higher but is unlikely to be lower (33). If one extrapolates these risks to the total number of plants plus noninsect animals and the total number of insects (25% and 10%, respectively), the total number of species threatened comes to be on the order of 1 million. Several sources of uncertainty, such as those around the total number of species on Earth, and whether the extinction risks of well-known groups are representative of less-well-assessed groups, in particular the enormous and poorly known group of the insects (96), make this number only an approximation. However, it is the most reliable and transparent global estimate available to date.

Considering extinction, together with species origination, is a natural phenomenon that has been occurring since life appeared on Earth, how high are these numbers compared with numbers expected from nonhuman causes and from rates in the past? Although the precise numbers for present extinction rates vary according to different time frames, taxonomic groups, and estimation methods and thus are difficult to compare with each other, scientific opinions converge on an overall wild species extinction rate that is at least tens to hundreds of times higher than the background rate (33, 95, 97) and is likely to be increasing rapidly (98) (**Figure 3**).

While a 50% chance of disappearing in the next 10 years (the average risk for critically endangered species) appears as an obviously high risk, some might think that the risk to vulnerable species (10% chance in 100 years) is low. To put these numbers in context, if a species were a 50-year-old human with a life expectancy of 80 years, a human in the nonthreatened category would have on average 30 more years to live, whereas a human in the vulnerable category would have approximately 1 week, and a critically endangered one would have as little as 3 hours (99). Put another way, think of how long it would take to lose half of the currently extant animal and plant species on Earth. Without human intervention (background extinction rates), it would take approximately 1 million years; if all species were in the vulnerable category, it would take 600 years to lose them, which is approximately 1,500 times faster than the natural extinction risk. If all animal and plant species were instead critically endangered, complete loss would take only 10 years, more than 100,000 times faster than the background extinction rate. Therefore, the overall extinction risk of threatened species is on the order of 1,000 to 100,000 times higher than the background extinction risk. The extinction risk of all species, threatened and nonthreatened, is of course much lower (99).

**5.2.2. A sixth mass extinction event?** There has been widespread media coverage of an ongoing sixth mass extinction (i.e., whether the present extinction magnitude and rate are similar to those estimated for the five major extinction events over Earth's history). A mass extinction is technically defined as the loss of at least 75% species over a relatively short period in geological time. The problem is that "short" is not easy to define; time spans of extinction events range from years for an asteroid impact to millions of years for episodes of enhanced volcanism. So, while it is easy to conclude that the magnitude of extinction observed is still far from the threshold of a mass extinction event, the rate is more difficult to compare. Barnosky and colleagues (98) calculated how long would it take for current extinction rates to produce a loss of mammal, bird, and amphibian species equivalent to those in the five mass extinctions. Depending on whether one assumes a pessimistic scenario (all species currently threatened go extinct within 100 years) or an optimistic one (only the critically endangered species go extinct over the next 500 years), extinction rates would be reaching mass extinction magnitudes within two to three centuries or 10,000 years or longer. Although what we are seeing today technically does not amount to a sixth mass extinction, whether we are on the brink of one depends on whether we think in human or geological timescales and also on our success in improving species' conservation status. But these technical issues, discrepancies,



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and uncertainties should not obscure the facts that (*a*) current extinction rates are higher than the average at any time in human history; (*b*) mass extinction magnitudes of species loss in the next few centuries cannot be ruled out; and (*c*) mass extinction is far from an inexorable process—human actions can make a dramatic difference as to whether such extinction rates are even reached.

**5.2.3. Trends in taxonomic diversity of local communities.** How is nature changing at much finer scales, from plots to landscapes? This is relevant because conservation and management actions tend to be implemented, and most of the functions of biodiversity and derived societal benefits delivered, at the local to regional scales. The wide scientific consensus on the decreasing trends in biodiversity indicators at the global scale does not extend to local assemblages. To what extent are local ecosystems increasing in taxonomic and functional biodiversity as a result of global species movement even while both native species and global biodiversity metrics decline? There is no agreement in the scientific community about whether the number of species in local communities shows a globally consistent trend. This disagreement is due to several factors, such as differences in spatiotemporal design, limitations in the methods of analysis and underlying datasets (103–106), and ecological causes. Among the last factor, a constant or nearly constant total number of species in many cases masks a balance between local losses and new arrivals of nonnative or native species. Weak global trends may be masking increasing trends in some regions (e.g., in temperate and boreal regions as a result of climate warming) and decreasing trends in other regions (e.g., in tropical regions as a result of land-use change). Some of the observed trends between only two points in time may represent oscillations rather than consistent directional trends. This discrepancy in findings is illustrated by two of the largest global analyses to date. One analysis, based on time series (repeated sampling of the same sites at different times) since around 1850 but with strong emphasis on the last few decades, and comprising a majority of marine organisms as well as some terrestrial and freshwater ones (107), shows no evidence of a consistent and widespread decline of species richness in local assemblages over time. The other analysis, based on a space-for-time substitution approach (a comparison of nearby sites that differ in land use but are assumed to be similar in other aspects) using data on terrestrial assemblages starting in the 1500s (108), shows an average decline of approximately 13%. More evidence and a better integration of methods are needed before more definitive conclusions can be drawn. Less controversial is the finding that, behind these trends (or lack thereof), the turnover in local species composition and relative abundance seems to be increasing as a result of an acceleration in both local colonization and extinction (107, 109).

Though relatively easy to monitor and useful as a rough approximation, species richness does not inform about changes in the abundance of populations or composition of communities. Because of this, other indices are used to monitor the state of biodiversity at these levels. Those most frequently used around the world show clear declining trends. For example, the Living Planet Index shows that the average change in abundance of over 20,000 monitored populations of over 4,000 species of amphibians, birds, fish, mammals, and reptiles has decreased 68% since 1970, with large differences among regions: 94% in Latin America and 24% in Europe (110). This finding is widely misreported as indicating that the abundance of all wild animals has decreased by 68% (111). The Biodiversity Intactness Index (BII) (112), which estimates the similarity between an area's terrestrial ecological communities (in terms of which species are present and their abundance) and the communities that would be there if there had been no human impacts, has fallen to a global average of 79% (33, 113); this 21% average change in ecological communities is greater than the average loss of species (13%, above) because it also reflects changes in species abundance. The BII detects changes in abundance (of both individual species and the whole assemblage) and it excludes increases in species number or abundance due to nonnative species. However, because it

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does not incorporate functional trait information, at least in its classical formulation, the BII does not differentiate between replacement of a species by a functional analog (which is unlikely to drive changes in ecosystem function) and replacement of a species by another species whose ecology is different (which may drive changes in ecosystem function). The rapid growth of functional trait databases may soon allow more direct estimates of changes in functional diversity.

**5.2.4. Changes in functional composition of local communities: functional diversity and homogenization.** The indices discussed above do not inform about another important way in which life on Earth is changing: The declining trends are not affecting different organisms in a homogeneous or random way. Rather, certain organisms are much more affected than others. This is because the functional traits (e.g., life span, reproductive strategy, morphology, physiology, lifestyle) of some organisms make them particularly vulnerable to human impacts, whereas other organisms, with opposite characteristics, thrive as a result of our activities. This process can happen in two nonmutually exclusive ways: First, humans involuntarily create habitat conditions that are distinctively favorable for some organisms but not others. For example, the frequently disturbed, nutrient-enriched soils in agricultural and peri-urban settings are ideal for ruderal plants to thrive and spread all over the world. Second, people deliberately target certain organisms either by extracting them (e.g., hunting, fishing, selective harvesting) or by nurturing and deliberately transporting them over long distances (e.g., garden plants, work animals, pets). While a comprehensive global stocktaking of the functional shifts in the composition of biological assemblages using a standard methodology is still lacking, evidence of functional shifts, particularly for vertebrates (114–119) and to a lesser degree for vascular plants (97, 118), is accumulating. As a broad generalization, within each trophic level, organisms that reach a large individual size, grow slowly, produce few offspring over their lifetime, and tend to tolerate resource scarcity more than physical disturbance are selected against, whereas organisms of small size and fast-paced lifestyle and whose fitness is more affected by lack of resources than by high disturbance and direct human presence tend to thrive around people and are transported over the world (120). The consistent decline of large, slowly growing organisms (the megabiota) such as large trees and animals is of particular concern, because they can have a disproportionate influence on key aspects of community dynamics and ecosystem function, from nutrient cycling to habitat creation to long-distance seed dispersal (68, 121–123).

## 6. CAUSES OF BIODIVERSITY DECLINE

What factors are behind the pervasive decline of nature? A distinction is made between direct drivers, which have direct physical impacts on nature, and indirect drivers, which operate diffusely by affecting the level, direction, rate, and/or intensity of direct drivers (124). Direct drivers can be natural (e.g., volcanic eruptions, earthquakes, weather events), human caused (e.g., deforestation, hunting, pollution, anthropogenic climate change), or a mixture of both (such as El Niño–Southern Oscillation phenomena or zoonotic diseases amplified by anthropogenic climate change). All indirect drivers are human caused, social, economic, demographic, cultural, institutional, and political in nature and ultimately underpinned by social values and narratives. They include patterns of supply and production of goods and services; patterns of consumption and technology adoption; dietary preferences; demographic dynamics; lifestyle choices and fashion trends; and institutions in the broad sense of socially shared rules, from local customary inheritance rules to international agreements such as the CBD and the World Trade Organization. The distinction between direct and indirect drivers is crucial conceptually and practically, because although direct drivers can be ameliorated or even temporarily stopped, these efforts are



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unlikely to succeed in the long term unless the indirect drivers, the root causes of the present decline in biodiversity, are tackled.

## 6.1. Recent Trends in Direct Drivers of Biodiversity Decline

The most comprehensive global systematic review to date (33, 125) shows that the most prevalent direct causes of nature's decline worldwide are land- and sea-use change (e.g., deforestation, expansion of agricultural frontiers, coastal development) and direct exploitation (e.g., hunting, fishing, selective logging), with climate change (e.g., changes in mean temperature, precipitation, and frequency and severity of extreme climatic events), pollution (including point-source organic and chemical pollution, seawater acidification by increased levels of $CO_2$ in the atmosphere, and light and noise pollution), and invasive species (introduced either voluntarily or unintentionally by humans or, much more rarely, arriving on their own) having less importance. This overall importance ranking of direct drivers changes according to realms and regions (**Figure 4**). For example, direct exploitation (mainly fishing) is the most important driver of biodiversity decline in the seas. Numerous more detailed and geographically restricted studies show that invasive species are a much more important driver in oceanic islands than on continents and that climate change is more important in Arctic and Mediterranean climate areas. Climate change has not been the most prominent driver of changes in nature at the global scale so far, but its impacts are growing and are likely to continue to grow during the rest of the twenty-first century (126–130). Two recent global studies, with a narrower and sharper focus on the distribution ranges of a wide set of marine organisms (131) and terrestrial amphibians, birds, and mammals (132), broadly agree with these conclusions.

Crucially, these drivers tend to act synergistically. For example, reef-forming corals can cope to some degree with seawater acidification, warming, local and remotely originated pollution,

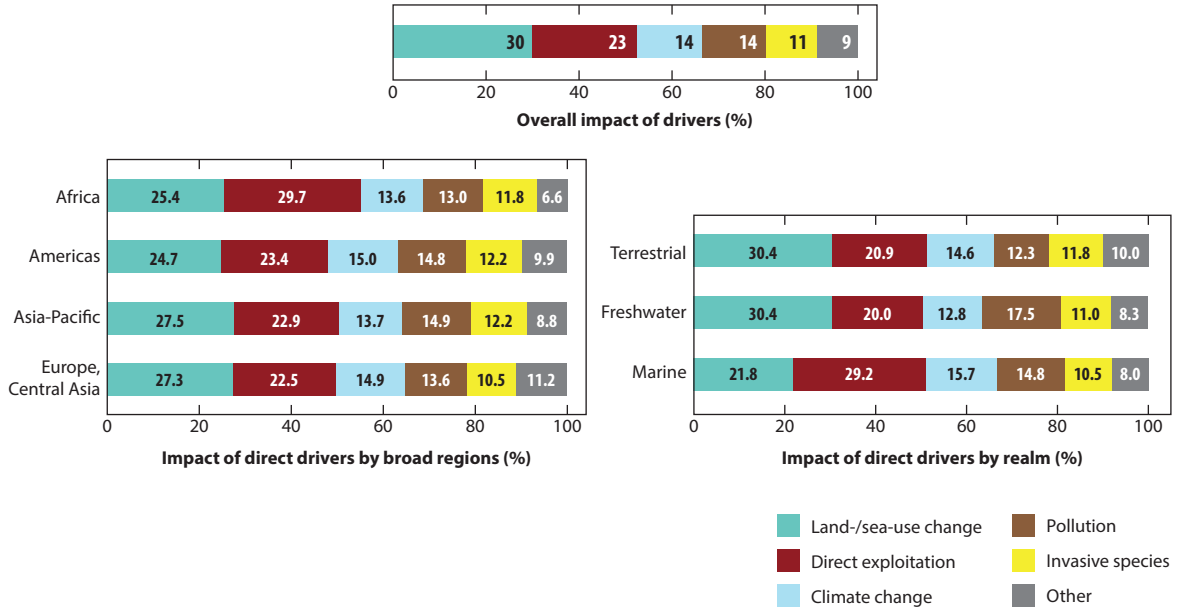



**Figure 4**

Relative impact of direct drivers of changes in nature since the 1970s, based on a global systematic review. Adapted with permission from Reference 33.



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and physical disturbance separately, but the combined impacts of these factors have catastrophic effects (128). As a land-based example, in the Amazon forest the synergy between global climate change (which caused increased occurrence of extreme drought events on top of a long-term warming trend), forest loss and fragmentation through agropastoral expansion, and increased fire use to manage pasturelands and clear forests is leading to large-scale fire events and associated biodiversity loss (133, 134).

## 6.2. Four Emerging Direct Drivers of Biodiversity Decline

The common direct drivers of diversity loss have been extensively covered in the literature, but several emerging drivers have only recently gained attention from the scientific community. While some direct drivers of biodiversity change are as old as humanity (e.g., burning, gardening for desirable wild plants, hunting of vulnerable species) or date back thousands (agriculture) or hundreds (chemical pollution) of years, others have emerged or dramatically increased in the past few decades. Prominent examples are plastic pollution, noise and light pollution, and seabed exploration and exploitation (a special case in the broad category of land- and sea-use change). Though vastly different in physical nature, these emerging drivers share some key characteristics: They are comparatively novel and therefore organisms have had little time to adapt to them, their magnitude is either already extremely high or rising steeply, and they involve telecoupled systems (see below). We examine these emerging direct drivers in the next subsections.

**6.2.1. Plastic pollution.** Since the 1950s, approximately 8,300 million tons of plastic (synthetic organic polymers) have been discarded, of which nearly 80% has ended up in landfills or the natural environment. Because they resist degradation through chemical or biological processes and tend to accumulate in sediments and organisms, plastics are a persistent as well as widespread form of pollution. The annual production [367 Tg year$^{-1}$ in 2020 (135)] approximates the total weight of the human population (136). Were this trend to continue, approximately 12,000 Tg of plastic waste would be in landfills or in the natural environment by 2050 (137). If spread evenly, this number would represent approximately 24 tonnes of plastic waste per square kilometer of land and sea surface, a level of pollution of any kind unprecedented in human history (128). Plastic pollution has numerous ecological effects. Images of sea mammals, birds, and turtles entangled in or choked with large pieces of plastic have captured the public's attention. Indeed, the strongest evidence of the harmful effects of plastics on the biota is associated with macroplastics, with more than 900 marine vertebrate and invertebrate species now affected by ingestion or entanglement (138).

However, a much more pervasive form of plastic contamination, whose effects are much less known and difficult to control, is that from microplastics and nanoplastics (particles less than 5 mm in length; hereafter termed microplastics). Microplastics are created by the weathering and breakdown of plastic objects, car tires, textiles, coatings, and additives to various products, and they are now found everywhere on the planet, including water, air, soils, and the bodies of many organisms (128, 136, 139). Their harmfulness is still poorly known due to technical difficulties in quantifying exposure and harm, uncertainty about how common in nature are the doses that have been found harmful in controlled experiments, and difficulties in tracking the many pathways through which they can cause harm (e.g., physical blockage, toxicity, inflammation, indirect effects through their additives or adsorption of toxic substances, replacement of food or chemical cues involved in feeding or mating behavior, bioaccumulation through trophic chains). Empirical evidence of negative effects on behavior, survival, and fitness of various organisms is accumulating (136, 140, 141), but reviews also show that no detectable effect is a response at least as common as harmful effect (141–144). The concentrations found in the environment are thus far considered



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below the threshold level known to cause harm in many locations, but if present trends continue (137), and with no realistic way of decreasing those levels once reached by using current technology, global exposure is projected to increase dramatically, with many locations going beyond these thresholds (143).

**6.2.2. Noise and light pollution.** Noise and light pollution are two other emerging pollutants. They act on organisms by disrupting environmental cues and thus are sometimes placed in the special category of sensory pollutants (145). Humans have been increasing the levels of noise and nocturnal light for centuries or even millennia, but the vast increases in magnitude and rate in the past few decades may overwhelm the adaptation capacity of many organisms. Although the influence of noise and artificial light can go well beyond the point source, unlike plastics their worst effects are expected to decline sharply once the sources are removed (146).

Noise pollution originates from urban dwellings, roads, industry, and aircraft and, in the oceans, from vessels, sonars, energy and construction infrastructure, and seismic surveys (146, 147). Because noise pollution is typically associated with other human activities that produce other potentially disrupting effects, such as light and chemical pollution or habitat disruption, testing its effects has called for inventive approaches. For example, an observational study using the carnival festival in Salvador, Brazil, as a proxy for high-noise treatment found decreased feeding and predator-fleeing activity in reef fish (148). An experimental study involved the playback of a phantom acoustical road to compare migratory bird habitat use, keeping all other factors constant (149). Noise pollution affects genetic and cellular levels, individual behavior, communication and fitness, and the structure of many communities of terrestrial and aquatic organisms, such as parasitic insects and fish and whales (146, 150–153). However, studies of noise pollution's impact on survival are far less numerous than those on behavior and physiology (146), and not all of these effects are associated with a clear net negative outcome. In addition, different taxonomic groups can be similar in their responses, suggesting most species respond to noise to some degree rather than a few species being particularly sensitive to noise (151).

Light pollution, compellingly described by Gaston and colleagues (154, p. 1132) as "erosion of natural darkness," is due to artificial lighting at night associated with the prolongation of human activity (work, recreation, travel, unmanned industrial operations) into the night hours. In addition to the direct effect of lighting infrastructure, skyglow—the brightening of the sky by upwardly emitted and reflected artificial light scattered in the atmosphere (155)—affects the nighttime sky sometimes hundreds of kilometers from the light source. Light pollution extends over 80% of the world, is disproportionately found in the Northern Hemisphere (155), and is increasing fast in spatial, temporal, and spectral extent (156). Areas that were lit for a long time, such as cities, are now under much brighter lighting and during much longer periods; areas on land and in the ocean that until recently were in deep darkness at night are now being lit. In addition, the spectral quality of artificial light is changing fast: Other sources of light are being replaced with solid-state light-emitting diode (LED) technology, which emits at a wider visible light spectrum, specifically the blue wavelengths, which are sensed by a wide variety of organisms (156).

The impacts of light pollution have been detected in microorganisms, fungi, invertebrates, vertebrates, and vascular plants. Light pollution affects, for example, the phenology, physiology, behavior, and in some cases population parameters of reptiles, birds, mammals (157, 158), and insects (159, 160). The effects are especially well documented in the case of night-flying migratory birds (158, 161, 162) and are expected to be particularly prominent on organisms used to living under low levels of light for long periods, such as those close to the poles (163) or those living in the ocean aphotic zone (deeper than 200 m) (164). The direction and intensity of the impacts vary widely and tend to be stronger (or better documented) at the level

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of individual physiology and activity and weaker toward the population and community levels (165).

The rise in extent, intensity, and range of noise and light pollution is well documented and their effects at the level of individual organisms appear widespread, but the literature on their population-level effects and especially on community-level cascading consequences in the field is much sparser. Intriguing examples such as altered plant dispersal due to noise alteration of bird behavior (166) and the indirect effects of light and noise on frog-biting parasites (147) suggest that the ecological cascades caused by these sensory pollutants deserve attention.

**6.2.3. Seabed exploration and exploitation.** The exploitation of seabed resources includes the extraction of polymetallic nodules (mostly manganese but also nickel, copper, cobalt molybdenum, and rare earth metals) from the abyssal plains, seafloor massive sulfides around the hydrothermal vents that form along oceanic ridges (mostly sulfides but also copper, gold, zinc, lead, barium, and silver), ferromanganese crusts (containing manganese, iron, and trace metals such as cobalt, copper, nickel, and platinum) (167) from the flanks of seamounts, and methane from gas hydrates from continental slopes and rises (168). This activity is only nascent: By early 2021, the International Seabed Authority (**https://www.isa.org.jm/**) had entered into only approximately 30 exploration contracts, none of them in the area of the ocean beyond national jurisdiction; official commercial exploitation had not yet started (168, 169); and much of the proposed activity is on the open ocean floor. This and the fact that the deep sea is a vast and largely unexplored area, representing approximately 50% of the Earth's surface and 95% of the biosphere's inhabitable volume (168), might lead to arguments that this activity is not much of a concern. However, seabed exploration and exploitation are clearly rising in the agenda of many sectors, both private and public, not least because the minerals extracted play an important part in the aviation and battery industries, and their extraction has been portrayed as a lesser evil and as a fundamental input in the transition to a low-carbon economy (169). Of particular concern is that the relatively small areas of the seabed with high mineral concentration also harbor unique, fragile, and poorly known biodiversity (170). The density of corals, anemones, sponges, and echinoderms in nodule-rich areas was more than two times higher than that in nodule-free areas, and some of the corals were found only in nodule-rich areas (171). Seamounts are also hot spots (or oases) of marine biodiversity and primary productivity and are used by pelagic fish, turtles, and mammals for feeding and resting (172–174).

Deep hydrothermal vents pose larger technological challenges for exploitation, but they are not free of risk, and they host organisms with an extraordinary degree of endemicity, estimated at 85% (170). They also display unique metabolic adaptations; many mollusks, tubeworms, and crustaceans living around hydrothermal vents feed on symbiotic chemosynthetic bacteria that thrive on the emissions from the vent. Two recently discovered examples eloquently illustrate how unusual vent life forms can be: The yeti crabs (*Kiwa hirsuta* and *K. puravida*) feed on chemosynthetic bacteria farmed on its claws (175), and the scaly-foot snail (*Chrysomallon squamiferum*) hosts symbiotic bacteria in an oversized esophageal gland that contribute to its nutrition (176). Deep-sea vents are also proposed as the most likely origin zone for all life on Earth and therefore have intrinsic value in terms of deep heritage of Earth's biosphere (177). Deep-sea organisms tend to have long life spans accompanied by extremely low growth rates. For example, the black corals (*Leiopathes* sp.) that live in seamounts near the Azores islands show a radial growth rate of 5 to 30 $\mu$m year$^{-1}$ and are estimated to live between 265 and 2,300 years (178). While these traits confer obvious selective advantages for survival at extreme conditions and low levels of resources, they make species highly vulnerable to disturbance. Indeed, the few studies carried out so far found that seafloor habitats take decades to recover following low-level disturbance (171; **https://www.eu-midas.net/**).



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Current seafloor mining technologies include massive physical disruption and release of toxic elements in situ and far-reaching sediment plumes and light and noise pollution (146, 168; **https://www.eu-midas.net/**). Researchers have been working on possible ways to minimize these impacts, whereas others are questioning the need to start immediately and are proposing a moratorium, taking advantage of the fact that this new kind of large-scale disturbance, unlike noise, light, and plastic, is not yet in full deployment, giving the opportunity to prevent damage instead of attempting to remediate it a posteriori (169, 179).

### 6.3. Recent Trends in Indirect Drivers

A large-scale quantitative ranking of indirect drivers similar to that of direct drivers depicted in **Figure 4** is not possible because indirect drivers tend to be diffuse and interact with each other in complex ways. However, their impacts have increased substantially since the middle of the twentieth century in both magnitude and geographical extent. The world's human population, which has nearly doubled since 1970, undoubtedly plays a role, but other factors that indirectly affect biodiversity have changed even faster: Global per capita spending has increased 13-fold (180), and global trade has increased by 900% (181). Diets have shifted considerably: Per capita consumption of land-based meat has roughly doubled since the 1960s (182) and that of fish and seafood has increased by more than 23% since 1998 (183). Nonfood consumer choices, such as fashion, mobile phones, recreation, and exotic pets, are also changing quickly. Global tourism, for example, has been growing at 3–5% per year (184).

Increasing asymmetries in the distribution of wealth have been associated with negative consequences for biodiversity (185–187). Income inequality at the global scale and among countries has decreased, but this has been driven by strong economic growth in a few countries with large populations (notably China), masking persistent inequalities in many other countries (188). Moreover, the contribution of within-country inequality to overall global inequality has risen (187, 188): As much as 38% of all additional wealth accumulated since the mid-1990s has been captured by the richest 1%, while the poorest 50% have captured only 2% of additional wealth (187). The share of wealth held by the private sector has increased at the expense of that shared by governments (187).

While the isolated effects of these socioeconomic factors on pollution, land-use change, climate change, and exploitation of organisms are well understood, they affect each other and often cancel or synergize each other's effects on direct drivers. Several technological advances have decreased the per-gram footprint of material consumption on biodiversity; meanwhile, planned obsolescence, fast turnover, and disposal models have increasingly dominated the consumer goods supply chains, often outweighing such advances. A few examples at increasingly wider scales illustrate this point: In rural China, while nature-based tourism and labor migration should each have a positive effect on local forest recovery, they partially cancel each other's impact, leading to a net effect that is still positive but smaller than their separate effects (189). Increasingly widespread nature- and climate-friendly practices associated with nature-based tourism around the world are outweighed by the rise in the number of emission-heavy international flights (184). More broadly, global public and private finance to foster biodiversity is estimated on the order of US$80–90 billion per year; at the same time, public support of activities that are potentially harmful to biodiversity is approximately US$500 billion per year (190).

In addition, because of the dramatic rise in international trade and globalization, impacts on nature in one place are often driven by choices, demands, and institutions in distant places. Conversely, consumers often do not suffer, or frequently are not even aware of, the ecological or social consequences of their choices. Although telecouplings—environmental and socioeconomic interactions over distances (191)—are part of the natural dynamics of Earth and have been accelerated by humans for millennia (80), they have been exacerbated since the 1970s (81, 185, 191). For better

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or worse, this increasing connectivity of materials, energy, information, wealth, waste, people, and other organisms across the globe is a hallmark of recent times. For example, the deposition of dust from Africa over the Amazon and the Caribbean has been occurring at varying rates for millions of years. However, changes in its amount, composition, and pollutant and pathogen loads due to land-use and waste-disposal practices, as well as climatic factors, over the past few decades have been proposed as factors with negative effects for marine communities (192). One-third of the threats to animals (193) and approximately 40% of natural resource extraction (194) worldwide are linked to international trade. Deforestation of tropical forests and worldwide illegal, unreported, and unregulated fishing are connected with the international corporate use of remote tax havens (195).

These complex entanglements between places, choices, and social actors might appear overwhelming. Rather than a reason for paralysis, however, they point to the need to tackle not only the direct local causes of nature's decline but also the socioeconomic factors fueling them. They illustrate why transformative change—fundamental, system-wide reorganization across technological, economic, and social factors, including paradigms, goals, and values (5)—rather than partial fixes at the level of symptoms is needed. Moreover, they stress the need to examine precisely how different socioeconomic factors, incentives, institutions, and organisms are embedded in the supply chain of good and services in order to devise long-lasting solutions for concrete biodiversity problems.

## 7. CONCLUSION

This article has taken a somewhat selective journey through what we see as some key or emerging issues in the arena of biodiversity. There has never been greater awareness of the global decline in biodiversity and its importance for Earth's functioning and humanity's well-being. Yet biodiversity remains a challenging term, a boundary object that spans a range of meanings and values but captures something essential to understand and nurture as we contemplate how to navigate toward a sustainable future entangled within the biosphere from which we spring.

### SUMMARY POINTS

1. Since its origin in the 1980s, the concept and use of the term biodiversity have evolved quickly and now have multiple dimensions.
2. Biodiversity has multiple values ranging across intrinsic, instrumental, and relational values, which differ strongly among social actors. Which of these values predominate or are even considered has a major influence on practical decisions about biodiversity.
3. Approximately 2 million species of living organisms are currently described; the total number of species on Earth is estimated, with much uncertainty, to be 10 million. Species-level diversity is dominated by terrestrial animals (especially arthropods), but marine and microbial systems contain a particularly rich phylogenetic diversity.
4. Humans have affected global biodiversity since prehistoric times both negatively (e.g., megafaunal and island extinctions) and positively (e.g., stewardship of organisms and ecosystems, creation of new ecosystems).
5. The reconfiguring of life on Earth at all levels, from genes to biomes, by humans is now evident. The rate of decline of biodiversity has intensified in modern times. Current extinction rates are much higher than prehuman ones. The extent and integrity of natural ecosystems; the functional, phylogenetic, and species-rich distinctiveness of local biotas



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across the world; the size of wild plant and animal populations; and the intraspecific genetic diversity of wild and domesticated organisms have all decreased.

6. The primary direct drivers of modern biodiversity decline include changes in the use of land, freshwater, and the oceans; increased harvesting of wild organisms; climate change; various forms of pollution; and invasive species. To date, climate change is a relatively minor cause of biodiversity decline but its impact is likely to rise greatly over this century. These drivers interact in complex ways, sometimes ameliorating and often reinforcing each other's effects.
7. The indirect drivers of biodiversity decline are increasing. Prominent among them are globally telecoupled consumption footprints, concentrated in certain countries and societal groups. Indirect drivers affect the rate and magnitude of preexisting direct drivers and give rise to new ones, such as plastic pollution, noise and light pollution, and seabed exploration and exploitation.
8. Addressing these underlying drivers requires bold system-wide rethinking and reorganization to put biodiversity at the center of societal values, planning, and goals.

## FUTURE ISSUES

1. Several emerging or neglected drivers of biodiversity decline warrant particular attention and study. These include plastic pollution, noise and light pollution, and seabed exploration and exploitation.
2. We need to better understand the biodiversity of novel ecosystems being created by biotic homogenization and climate change and to better contextualize the trade-offs and tensions between place-based biodiversity values (e.g., native species) and functional values (e.g., resilience of whole ecosystems over levels of species diversity).
3. The multiple values of biodiversity, and its multiple valuers, including local traditional and Indigenous communities, need to be better incorporated into global framings of biodiversity.
4. Many frontiers of biodiversity, including tropical forest canopies, species-specific mutualists or parasites, gut microbiomes, the seafloor and soil sediments, and deep biosphere microbial communities, are still poorly explored.
5. We need a more refined understanding of how different components in the fabric of life interact with planetary function, such as maintenance of resilience to extreme events and climate change, as well as underpinning finer-scale contributions to different people across the world.
6. We need to better understand how to fully embed biodiversity into societal values, policy planning, and decision-making to enable the systemic shift required to reverse the ongoing decline.

## 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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IPBES Global Assessment Report on Biodiversity and Ecosystem Services: **https://ipbes.net/global-assessment**

Catalogue of Life: **https://www.catalogueoflife.org/**. An online database that provides an index of known species across the seven kingdoms of life.

OneZoom: **https://www.onezoom.org/**. A rich visual exploration of the tree of life.

CBD (Convention on Biological Diversity): **https://www.cbd.int/**

Our World in Data: **https://ourworldindata.org/biodiversity**. A rich set of trusted resources around biodiversity data and their interpretation.

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