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ant-following birds is one noticeable consequence of *E. burchellii* vacating forest fragments. Some thirty species have evolved to track *E. burchellii* as it carries out swarm raids through the forest. The birds form populous, mixed-species flocks that are specialized to hunt arthropods flushed from the leaf litter. An analogous avian fauna has evolved in association with *Dorylus* army ants in Africa; in the Kenyan rainforest, fragmented landscapes similarly fail to sustain populations of ant-following birds.

Abundances of myrmecophyte plants also decrease markedly in forest fragments, making these mutualisms prone to stochastic, local extinctions. Compounding all of these impacts, regeneration of the forest is no guarantee of community restoration: secondary regrowth lacks the rich diversity of ants found in primary forest, implying that ants and their associated species may be amongst the most vulnerable organisms to habitat shrinkage and fragmentation. The few existing population genetic studies of myrmecophiles add further weight to this inference: populations of the lycaenid *Phengaris alcon* and myrmecophilous hoverflies of the genus *Microdon* are spatially disjunct, highly inbred, with extremely small estimated effective population sizes. Myrmecophiles with potentially poorer dispersal abilities, such as many beetles, may be still more precariously positioned. How will these species, along with the myriad others whose livelihoods are directly or indirectly affected by ants, fair as our planet continues to warm? The composition of ant communities is predicted to shift at a global scale, the gears already in motion, as thermally tolerant species and those from warmer habitats spread at the expense of more vulnerable species. If we are to nurture our own mutualistic relationship with these miniscule sculptors of the biosphere, there is an urgency to better understand the details of their relationships with other life forms.

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Primer

Invertebrate biodiversity and conservation

Nico Eisenhauer[1,2] and Jes Hines[1,2]

Biodiversity is changing at alarming rates as a result of human activities; yet biodiversity is the basis for ecosystem services upon which humans depend. Most of what we know about past, current, and projected biodiversity trends, as well as the ecosystem consequences of biodiversity change, is based on charismatic species, mostly plants and vertebrates. But 31 out of 32 animal phyla are invertebrates, representing roughly 75% of all described species on Earth. Evolution has not only produced an astonishing taxonomic diversity of invertebrates, but also an unparalleled morphological and functional diversity that has allowed invertebrates to populate marine, terrestrial, and freshwater realms. Invertebrates are responsible for many ecosystem services and disservices, which makes their appreciation and conservation a top priority of future research and policy.

In this Primer, we describe the diversity of invertebrate life on Earth and briefly summarize the evolutionary history of invertebrates. We highlight several ways that invertebrates influence the functioning of ecosystems and, consequently, human nutrition and health. Through their manifold effects on ecosystems, humans are changing invertebrate communities and, by extension, the balance between services and disservices provided by invertebrates. Given recent reports on dramatic changes in invertebrate diversity, as well as current major data gaps in the temporal and spatial distribution of invertebrates, we highlight the need for future research to identify and address drivers of invertebrate diversity. Such research focused on invertebrate biodiversity will contribute to the informed conservation actions and legislation that are required to maintain and improve ecosystem functioning.

Form and phylogeny

One of the most remarkable features of the planet Earth is the incredible diversity of life found upon it. Invertebrates comprise more than 1.25 million documented species, making up almost 95% of the species in the animal Kingdom (Figure 1). That number is increasing as more species are described. Vertebrates (i.e. Chordata) make up one phylum in Animalia, and the remaining 31 phyla contain invertebrate taxa, such as mollusks (chitons, snails, bivalves, squids, and octopuses), annelids (earthworms and leeches), and cnidarians (hydras, jellyfishes, sea anemones, and corals) (Figure 1). Among these, the most diverse invertebrate phylum is Arthropoda, which contains ~1.11 million described species (Figure 1). Roughly 85% of arthropods are insects, and this phylum also includes arachnids, crustaceans, and myriapods (Figure 1). Collectively, invertebrates constitute most of the diversity of animal life on Earth as we know it.

Whereas some taxa that we are familiar with today have ancient origins, others appeared more recently in geological history (Figure 2). The earliest known animals were Cnidarians, such as primitive jellyfish, that appeared in the fossil record 580 million years ago. Fossil evidence of mollusks and more complex animals exists as far back as the early Cambrian (540 million years ago). Some lineages of invertebrates have persisted through five major mass extinctions, and the rise and fall of more recent animals, such as dinosaurs, which occurred during the time span from the Permian to the Cretaceous (up to 300–200 million years ago). Other lineages, such as Trilobites, are now entirely extinct (Figure 2).

In part because of their long evolutionary history, invertebrates exhibit an astounding degree of morphological and functional diversity, including the major changes that allowed them to move beyond their marine origins to invade terrestrial and freshwater realms. The members of almost half of the 31 invertebrate phyla are entirely marine, and the members of the remaining phyla are found primarily in marine and, to a lesser extent, freshwater or terrestrial habitats. Given the aquatic origin of invertebrates, major adaptations to terrestrial life include features allowing gas exchange without desiccation. Most invertebrates are sensitive to changes in precipitation, temperature, and salinity, and access to water and air play major roles in determining the structural, physiological, and behavioral characteristics displayed by invertebrates living in all realms.

Terrestrial invertebrates have been particularly sensitive to plant chemistry and morphology. In several cases, invertebrates have gone through adaptive radiations together with flowering plants. This co-evolutionary

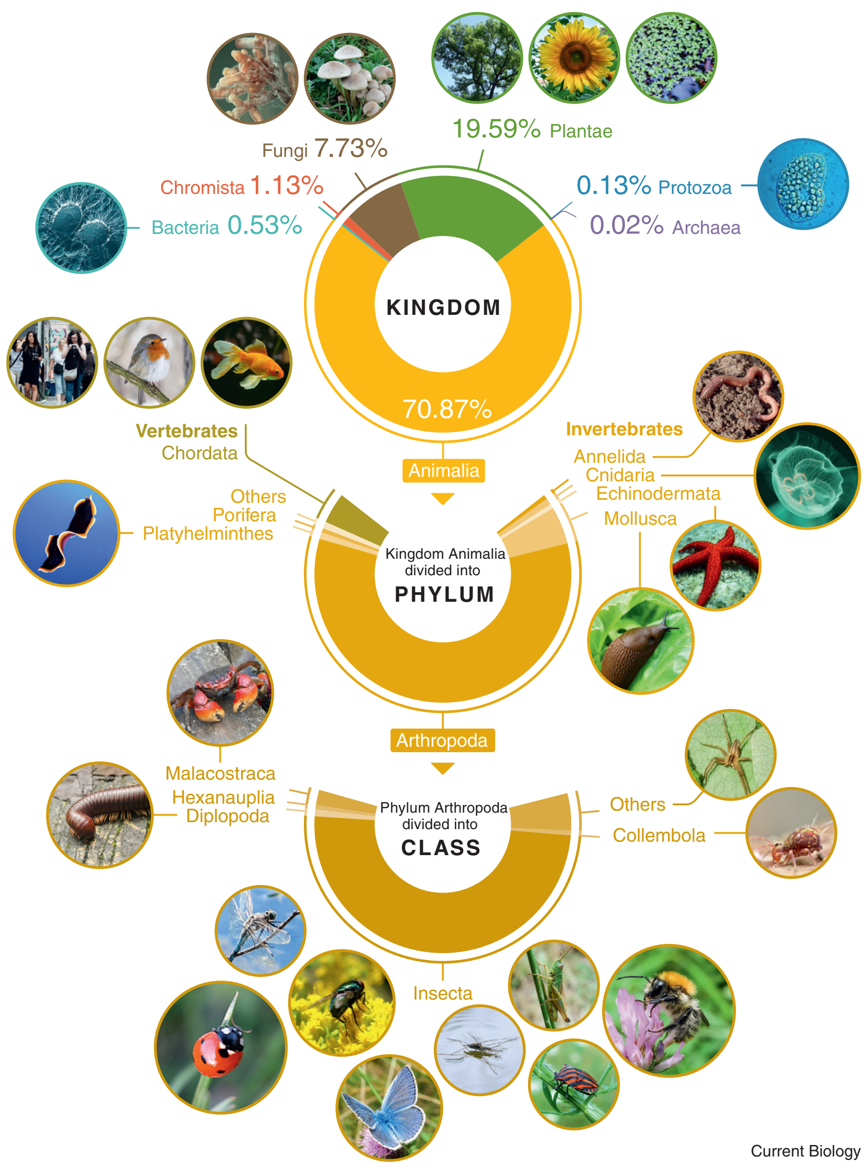

Figure 1. The diversity of life on Earth.
According to the Catalogue of Life (https://www.catalogueoflife.org/), there are currently 1,896,632 described species on Earth. This pie chart illustrates the proportions of major groups of organisms (according to kingdom). For animals, we also show phyla, and for arthropods we show classes. Image credits (clockwise): Plantae images: Gabriele Rada/iDiv; Protozoa: Colpoda_inflata Dr. Eugen Lehle (CC BY-SA 3.0), via Wikimedia Commons; Annelida, Cnidaria, and Echinodermata: Pixabay; Mollusca and others: Gabriele Rada/iDiv; Collembola: Andy Murray; Insecta images: Gabriele Rada/iDiv; Diplopoda: Freepik; Malacostraca and Platyhelminthes: Pixabay; Chordata humans: Pixabay; Chordata bird: Gabriele Rada/iDiv; Chordata fish: Pixabay; Bacteria: Pixabay; Fungi: Mycorrhizal_root_tips_(amanita) Ellen Larsson, (CC BY 2.5), via Wikimedia Commons; Fungi: Gabriele Rada/iDiv.

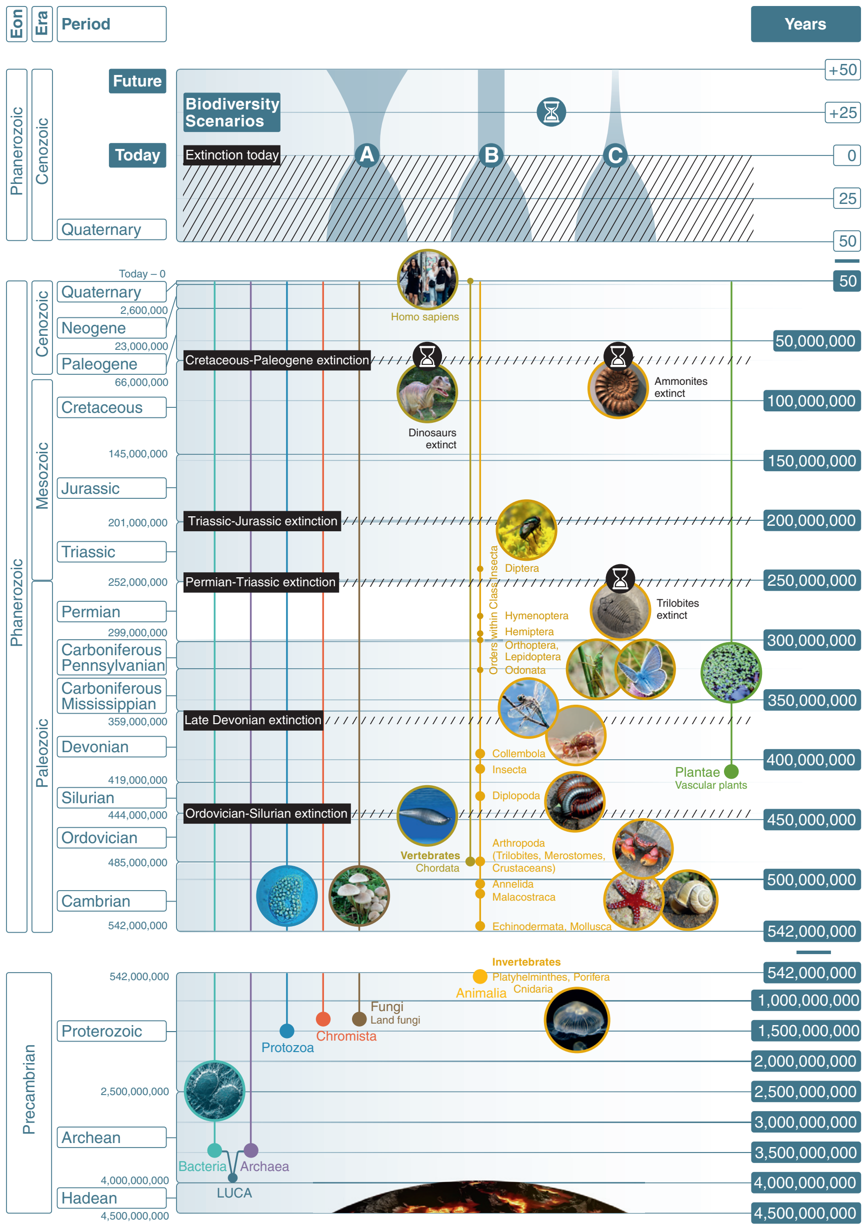

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Figure 2. Earth's history, the Anthropocene, and future scenarios.
Earth's history has seen a tremendous diversification of life, but also multiple major extinction events. Invertebrates appeared very early on (Precambrian) and nowadays dominate the diversity of life on Earth. With the appearance and intensifying activities of humans, many invertebrate species are threatened by extinction. Our decisions, policies, and conservation actions will determine the fate of invertebrates. Dots on lines depict estimated appearances of taxa based on fossil records. Image credits (left to right, top to bottom): Bacteria: Pixabay; Protozoa: Colpoda_inflata Dr. Eugen Lehle, (CC BY-SA 3.0), via Wikimedia Commons; Fungi: Gabriele Rada/iDiv; Hadean: Pixabay; *Homo sapiens* and dinosaurs: Pixabay; Vertebrates: Metaspriggina_NT Nobu Tamura, (CC BY-SA 4.0), via Wikimedia Commons; Diptera and Odonata: Gabriele Rada/iDiv; Collembola: Andy Murray; Diplopoda and Cnidaria: Pixabay; Orthoptera: Gabriele Rada/iDiv; Ammonites and Trilobites: Pixabay; Lepidoptera: Gabriele Rada/iDiv; Crustaceans and Echinodermata: Pixabay; Mollusca and Plantae: Gabriele Rada/iDiv.

history means that many plants that humans rely on, for example for food, medicine, or shelter, in turn rely on invertebrates, for example, for pollination. Considering their long persistence, in comparison to humans, which originated within the past 300,000 years, as well as their functional diversity, led entomologist E.O. Wilson to proclaim "We need invertebrates, but they don't need us."

Functions

Invertebrates provide many ecosystem functions and services. However, there are also numerous disservices related to the activities of invertebrates. To illustrate the mixed blessing of invertebrate diversity, we list some examples in the contexts of human health, agricultural production, human nutrition, as well as decomposition and nutrient cycling (Figure 3). For instance, the milky-blue blood of horseshoe crabs (Figure 3A) provides the only known natural source of limulus amebocyte lysate. This substance plays a unique role in pharmaceutical development, in contexts ranging from vaccines to artificial joints, as it detects an endotoxin that can be deadly to humans. However, many invertebrates can also act as vectors of diseases, such as malaria (caused by *Plasmodium* that is transmitted by mosquitoes), Chagas disease (caused by *Trypanosoma cruzi* that is transmitted by kissing bugs), and Lyme disease (caused by *Borrelia* that are transmitted by ticks; Figure 3B).

In the context of agricultural production, invertebrates provide beneficial services, such as pollination (mostly bees) and natural pest control (by predators like spiders and beetles; Figure 3C), while other invertebrates act as pests limiting crop production (for example, plant-feeding nematodes and insects like potato beetles) (Figure 3D). Moreover, many invertebrates are nutritious components of human diet (for example, seafood; Figure 3E), but they can also have detrimental effects on human health by acting as endoparasites (for example, tapeworm in human gut; Figure 3F). Most of the primary production (in some ecosystems >90%) is not actually consumed by herbivores, but ends up in the 'brown' energy channel of decomposition — this massive amount of producer biomass gets consumed and processed by decomposer communities. Several invertebrate groups drive decomposition and nutrient cycling by fragmenting litter and mineralizing nutrients, or by feeding on microorganisms (which is why earthworms are often referred to as 'gardeners' friends'; Figure 3G). On the other hand, decomposers can also provide disservices by damaging human properties (as with termites decaying wooden constructions; Figure 3H).

Notably, human-induced environmental changes have been shown to influence the balance between services and disservices. For instance, while agricultural plant monocultures often experience high rates of above-ground and below-ground herbivory and thus reduced biomass production for livestock, high-diversity plant communities foster natural pest control by promoting invertebrate predators of herbivores. Moreover, beneficial effects of invertebrates often dominate in their native ranges, because complex ecological interactions had time to develop, while many undesired impacts come into effect when humans actively or passively (for example, through climate change) spread invertebrates that can become invasive. Moreover, effects seen in one ecosystem or ecosystem compartment can be due to changes in invertebrate diversity in adjacent ecosystems. That is to say, invertebrates can have far-reaching effects on multiple ecosystem functions (ecosystem multi-functionality). This is because many invertebrates connect different ecosystems or compartments through their mobility and/or life stages, such as terrestrial and aquatic ecosystems, streams and lakes, as well as above-ground and below-ground compartments. For example, many terrestrial invertebrates have larval stages in the soil or in water, while the services of adults may be mostly observed above ground. To understand and predict how changes in invertebrate communities will affect the balance between ecosystem services and disservices, a multi-trophic cross-ecosystem perspective is needed. The functional significance of invertebrates (Figure 3) motivates calls for conservation actions.

Figure 3. Services and disservices of invertebrates.
Invertebrates provide services and disservices in diverse contexts. Examples related to human health: (A) blood of horseshoe crabs used in pharmaceutical development; (B) ticks transmit lyme disease. Examples in agricultural production: (C) predators provide natural pest control; (D) herbivores can act as major crop pests. Examples in human nutrition: (E) seafood; (F) parasites impede human nutrition. And examples involving decomposition and nutrient cycling: (G) earthworms contribute to the mineralization of organic matter; (H) termites can damage human structures. Image credits: (A,D,E) Pixabay; (B,H) Freepik; (C) Krabbenspinne-CC-BY-Anina C. Knauer; (F) AdobeStock.

Futures

Invertebrates have attracted a lot of public and political attention recently, due to reports on significant declines in invertebrate abundance, biomass, and diversity across the last decades. While such dramatic reports have dominated the public discourse, subsequent research has suggested that a more nuanced view on biodiversity changes is required. For instance, changes in invertebrate diversity may depend on the ecosystem realm, for example with the abundance of terrestrial insects having declined by ~9% per decade, while the abundance of freshwater insects has increased by ~11% per decade since 1960. However, data on invertebrate diversity trends are still scarce and biased towards some terrestrial flying insects, while other aquatic and soil invertebrates are strongly underrepresented on the IUCN Red List.

To conserve invertebrate diversity, it is essential to identify the drivers of divergent biodiversity trends. There is empirical evidence that land-use change, landscape simplification, and elevated urbanization, including habitat loss and chemical pollution, are essential drivers of terrestrial invertebrate diversity decline. By contrast, enhanced abundances of freshwater insects may be explained by the recovery from past degradation related to the *Clean Water Act* and other legislation, increased climatic warming, as well as elevated productivity in response to eutrophication. However, these drivers often co-occur and have interactive effects, which is why data in hand on single-driver effects may have limited capacity to predict future changes. Future research will benefit from standardized invertebrate diversity monitoring across environmental contexts, especially when monitoring is paired with targeted experiments on interacting global change drivers. Moreover, to appreciate the ecosystem consequences of changes in invertebrate communities, much more research is needed that manipulates

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these communities according to environmental and biodiversity change scenarios.

Notably, many terrestrial protected areas (for example Natura 2000, wilderness areas, national parks) may not have been established with a particular focus on invertebrates, and may have limited benefit for key groups, such as soil invertebrates. More tailored conservation actions may be required to maintain and restore (soil) invertebrate biodiversity. While there is the urgent need for future research to better inform such conservation actions and legislation, there is no time to lose, and current knowledge should already be applied in ecosystem management to shape biodiversity trajectories (Figure 2). Recent data on freshwater abundance trends indicate that such targeted nature conservation measures can indeed be successful in restoring biodiversity. However, given the wide variety of environmental impacts that the human population exerts on ecosystems around the world, more and more scientists are convinced that only a transformative change of human behavior and appreciation and living together with nature will be able to create better futures for people and the planet.

Sparked by rising public attention and pressure to combat climate change and safeguard biodiversity — illustrated for example by the global climate strike movement *Fridays for Future* — there have been recent actions to foster biodiversity monitoring and conservation, such as the *EU Green Deal*. In support of such initiatives, many methodological developments provide promising avenues for future research. For instance, scientists have been developing *biodiversity stations*, similar to weather stations, for the standardized and continuous monitoring of biodiversity, and molecular tools to assess biodiversity are getting more sophisticated and broadly applicable. Combined with cutting-edge techniques like deep-learning and computer vision, it will be possible to improve and validate image-based taxonomic identification and to develop public, curated reference databases for the analysis of invertebrate diversity trends and the identification of main drivers of change. The case of invertebrates illustrates that biodiversity assessments and conservation have to take a whole- as well as cross-ecosystem perspective — a comprehensive appreciation of the ecological connections across ecosystem boundaries. Better-informed biodiversity scenario modeling will help to identify particularly vulnerable and threatened areas and can then guide conservation actions. Early in the *UN Decade on Restoration*, invertebrates on every continent and in every ocean have to be in the focus to halt and reverse the degradation of ecosystems.

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Primer

Wildlife trade

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Global trade of wildlife is a major driver of species decline. The trade in wildlife actually plays a much larger role in our daily lives than many people realize, and its use and legality are surprisingly complex. Wildlife trade includes the trade of any organism, including fungi, plants and animals, sourced from the wild. This comprises thousands of wild species, including over 7600, or nearly one quarter, of terrestrial vertebrate species. Trade in wildlife is worth billions annually via commercial fishing at $180 billion, timber at $227 billion and fashion at $2.5 billion — in addition to largely unquantified trade for meat, medicine, ornamental use and pets. Wildlife trade, such as that of ivory, is the subject of intense public debate, international regulation and criminal prosecution, while trade of other species is more often overlooked. How wildlife trade is regulated and what is legal and illegal varies both between and within taxonomic groups and depends on where and how trade occurs. Wildlife trade across most sectors has increased since monitoring began, for example, between 1996 and 2018 the global fish market rose from $40 billion to $180 billion, wood from $65 billion to $137 billion and reptile leather for fashion trade from $140 million to $600 million. In concert, the annual number of trades legally traded through CITES has also grown, from under 5000 transactions in 1977 to peaking at over 1.3 million in 2015, with shipment size increasing in parallel and seizures of illegally traded species showing similar trends. Balancing the needs of people for livelihood generation, especially with access and benefit-sharing rights, with the impact on species survival remains difficult. Issues like the role of trophy and sports hunting within conservation remain a topic of debate in the conservation community. Finding approaches that enable long-term species survival, are equitable and do not undermine livelihoods is a constant challenge.