



Impacts of Anthropocene Defaunation on Plant-Animal Interactions

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Learning Objectives

This chapter will help readers to:

- Become familiar with the term Anthropocene and some of its impacts on plant-animal interactions
- Understand what contemporary defaunation means and why it has considerable consequences on the diversity of interactions between plants and animals
- Foment awareness of the anthropogenic threats to biodiversity and species interactions and the significance thereof for human wellbeing

13.1 The Anthropocene, an Epoch of Distinguishable Human Footprint on the Planet

The 1977 Nobel Laureate in Chemistry, Paul Crutzen, has championed the use of the term “Anthropocene”. In a short paper (Crutzen 2002), this prominent scientist argued that the omnipresent and intense impact of the human enterprise on the planet demanded global recognition that the characteristics of the Holocene bore such a formidable anthropogenic footprint that it should be replaced with the term Anthropocene. Although not free of debate (see Zalasiewicz et al. 2011), the term has percolated considerably not only among the scientific community, but also in other branches of academy and, indeed, society at large. Presently, for example, at least two periodicals carry the term: Anthropocene (a print and digital magazine produced under the auspices of *Futureearth* – ► <https://www.anthropocenemagazine.org>) and The Anthropocene Review (from *Sage Journals* – ► <https://journals.sagepub.com/home/anr>). Among the 171 neologisms appearing in the 2014 edition of the Oxford English Dictionary, Anthropocene is featured therein, and the entry reads “*the era of geological time during which human activity is considered to be the dominant influence on the environment, climate and ecology of Earth.*” Dictionaries for other major languages have followed suit, further confirming the penetration of the term into the lexicon of society at large. We propose, therefore, that an examination of our understanding of the status of biodiversity in contemporary time needs to consider plant-animal interactions in the Anthropocene—as the chapter’s title indicates.

The manifestations of the Anthropocene are multiple and, naturally, encompass a host of both socio-economic and environmental variables. A comprehensive review of the manifestations and trajectories of the Anthropocene (Steffan 2015) depicts an evident pattern of what therein is referred to as the “Anthropocene’s great acceleration,” whereby such variables exhibit a steep increase, particularly manifested roughly over the last five decades of the last century and until now. Leaving the socio-economic variables aside, the environmental variables of this prominent paper, include several trends of biogeochemical nature (particularly relevant to climate change) and three that are most critically related to the subject matter of this chapter:

1. tropical forest loss (measured as percent forest coverage loss);

2. “domestication of land” (total terrestrial area converted to human-dominated landscapes);
3. “terrestrial bio-degradation” (the estimated mean percent decline in species abundance).

As we will elaborate below, these have important bearings on the disruption of ecosystem processes, but none of the trends of this important review considers the trajectory of species interactions (such as plant-animal interactions) in the Anthropocene.

Let us consider, first, the trends of tropical forest loss and land domestication of Steffen’s (2015) great Anthropocene acceleration. When biologists, ecologists and conservationists call attention to anthropogenic destruction or degradation of natural ecosystems and the loss of biodiversity, they are not exaggerating. Deforestation, soil degradation, water and air pollution, and uncontrolled fires caused (directly and indirectly) by human activities are nowadays at dramatic levels. Sadly, examples are vivid and abundant. For example, the Annual Report on Deforestation in Brazil (MapBiomes 2020) revealed that the Amazon lost an average of 2110 hectares of forest per day in 2019 – an area equivalent to about 2000 football fields. This biome was the most devastated in the country, representing 63% of the 3339 hectares felled per day in the entire country. Considering deforestation of all six major Brazilian biomes, Earth lost 1,218,708 ha of natural vegetation in 2019. In this assessment, the two best-monitored biomes in Brazil are the Amazon rainforest and Cerrado, and these accounted for 96.7% of the total deforested area detected for the country in 2019 (MapBiomes 2020; ■ Figs. 13.1 and 13.2). This figure is alarming, given that the Amazon harbors the greatest density of biodiversity on Earth, and the Cerrado holds the greatest biodiversity among savanna-type ecosystems in the world (Oliveira and Marquis 2002).

Let us now consider the case of fires, an increasingly impactful driver of forest area loss. In the Brazilian state that concentrates the largest portion of preserved Amazonian forest, Amazonas State, Brazil’s INPE (Instituto Nacional de Pesquisas Espaciais) tracks fires and deforestation using multiple satellites equipped with optical thermal sensors (INPE 2020). A time-course of incidence of fires readily shows that they are increasing and consistently surpassing the 22-year average number of 10,000 events since 2015 (■ Fig. 13.1). Furthermore, in the first 8 months of 2020, fires in the Brazilian Amazonian forest and in the forests of neighboring countries, as well as in the Cerrado savanna and the Pantanal wetlands are surpassing historical records (INPE 2020; MapBiomas 2020). As broadly publicized in international media, year 2019 (e.g., in Australia), and year 2020 (e.g., in California, Colorado, Brazil) was characterized by a dramatic increase in number and intensity of fires around the world, moving us into what appears to be a strong companion (and, perhaps, name-competitor) of the Anthropocene—a sort of “Pyrocene” epoch. Sadly, Brazil’s case is not unique, and deforestation and fire also are ravaging extensive areas of Africa, North America, Europe, Australia and Asia.

In terms of the proximate drivers of land domestication and tropical forest loss, conversion to agriculture, cattle ranching, massive logging and mining are predom-

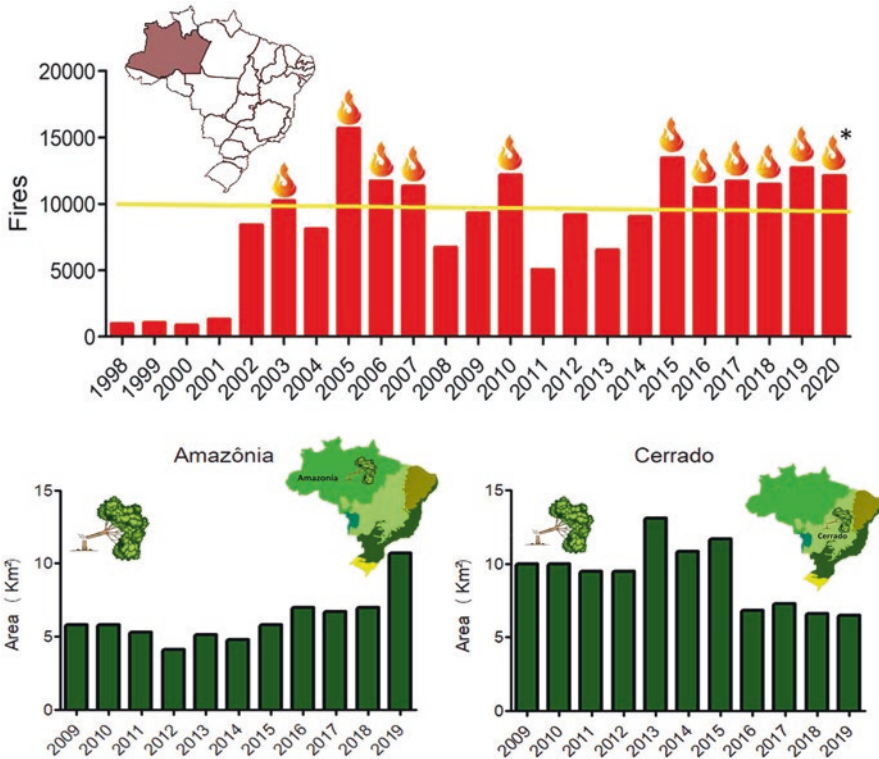


Fig. 13.1 Annual incidence of fires (upper panel) monitored by INPE in the Amazonas state (color-highlighted on the map), Brazil. The original data were derived from ► http://queimadas.dgi.inpe.br/queimadas/porta-static/estatisticas_estados/. *Year 2020 includes only the period January–August. Deforestation trends (lower panel; in thousands of km²) in the two best monitored Brazilian biomes: Amazonia (left) and Cerrado (right). The original data are available for public use and consultation at INPE/PRODES – Terra Brasilis (► <http://terrabrasilis.dpi.inpe.br/app/dashboard/deforestation/biomes/amazon/increments>)

inant and they have devastating effects on the diversity and structure of the targeted ecosystems.

The quantification and monitoring of the subsequent spatio-temporal dynamics of the areas impacted by these anthropogenic drivers should be technologically feasible given the increasing sophistication and availability of remote sensing tools. This, and the fate of areas currently set aside for biodiversity conservation should inform us of the status and trends of the vegetation in the Anthropocene. Such technology, however, can only partly or indirectly provide information of biodiversity as a whole, since the current situation and trajectories of animal communities –that is, the current and future trends of defaunation– are at least partly overlooked. Therefore, assessment of the conservation status of plant-animal interactions, needs to carefully examine the defaunation trends.

Regarding the immediate biodiversity consequences of the recent pulses of deforestation and fires, preliminary reports provide a gloomy picture. For example,



■ **Fig. 13.2** The Brazilian Tropical Savanna, Cerrado. The images show the same area of Vereda (above) and cerrado sensu stricto (below), before and after fire occurrence. Municipality of Uberlândia, MG, Brazil

Australian scientists who have considered the possible faunistic impacts of the 2019–early 2020 fires in that country reached an estimated number of over 800 million animals killed in New South Wales, and over 1 billion nationally (Ward et al. 2020). Long-term studies are needed for this and other fire- and deforestation-impacted parts of the world, and very likely will be conducted over the next few years, but it will be critical to also examine, via careful monitoring, the possible patterns of animal recolonization into the wild areas impacted by land use change (including fire, ■ Fig. 13.2), as well as into the areas that are not permanently assigned to agricultural activities for food production and livestock maintenance. In the meantime, we can use the currently available information to gather a picture of our current understanding of defaunation in the Anthropocene, as we discuss next.

13.2 Defaunation in the Anthropocene

The word “defaunation” in a sense of animal removal from a community due to human activities (“anthropocene defaunation” sensu Dirzo et al. 2014), has its origins in the elegant work of Simberloff and Wilson (1969). In their classic experi-

mental manipulative study, the authors applied insecticide onto small islands in the Florida, USA to remove the entire assemblage of arthropods, and examine the recolonization patterns and effects on the plant community. In the decade of 1980, Janzen and Martin (1982) suggested that the extinction of the Pleistocene megafauna generated “plant anachronisms” to explain the occurrence of traits (e.g., extremely hard fruits, or very spiny fruits and stems that protect relatively small-sized seeds) among many Neotropical trees that cannot be understood if one does not consider their interaction (i.e. seed dispersal) with such extinct megafauna. Such animals likely were important selective forces leading to the evolution of these anachronistic traits. These initial studies highlighted the impact that animal extinction could have on plant communities and in the biodiversity of entire communities. Several years later, in the 1990’s, a study considering two tropical forests with contrasting degree of conservation, performed a detailed comparative analysis of the impacts of reduced abundance and diversity of understory mammalian herbivores on the plant community (Dirzo and Miranda 1990). This study presented for the first time the notion and the term “contemporary defaunation”, showing the current negative impact of the human enterprise on the animal community, and its impacts in the structure and diversity of tropical plant communities. Presently, we see the use of the term defaunation and its different facets to describe the status of animal communities under anthropogenic disturbance and the patterns and consequences thereof on plant communities and ecological processes, including species interactions at local and global scales (Dirzo et al. 2014; Young et al. 2016).

13.3 Drivers and Magnitude of Defaunation

Defaunation is a useful entry way to examine the “terrestrial bio-degradation” variable of Steffen’s (2015) great acceleration of the Anthropocene. Recent reviews (e.g., Young et al. 2016) indicate that the main direct driver of defaunation is over-exploitation (hunting, and illegal trading). Land use change, as we have discussed above, is the most critical indirect defaunation driver, followed by invasive taxa and toxication and, already detectable, but undoubtedly more prominently in the future, climate change. Although the number of globally extinct species of vertebrates may seem small, i.e., ~700 since year 1500, ca. 60% of the extinctions occurred since 1900, clearly revealing an accelerated trend, and representing values that are 2–3 orders of magnitude higher (depending on the group of vertebrates) than background extinction rates (Ceballos et al. 2015). Nevertheless, for the purposes of this chapter, our main concern here is the decline in the local abundance of animals, as this facet of defaunation can reveal the impacts on plant-animal interactions (Dirzo et al. 2014). Monitoring of a robust number of animal populations across the globe (although with important geographic biases, particularly under-representation of tropical regions), suggests that over the last four to five decades, abundance of vertebrates has declined by about 50% (Dirzo et al. 2014), with more recent reports elevating the figure to as much as 68% (Live Planet Report, WWF 2020). Although these analyses do not consider the populations of species that are increasing (which would be informative of species turnover and net changes in animal communities,

see Dornelas et al. 2019), they provide a picture of considerable decline. When declines at given locations become extreme, they lead to an alarming problem of population extinctions. Assessments of the possible magnitude of global population loss are still in their infancy, yet available studies indicate an alarming situation. For example, using a sample of 177 species of mammals, Ceballos et al. (2017) estimated that over the period 1990–2015, close to 50% of the examined species had reduced their distribution range by 80% or more, therefore implying a dramatic loss of populations, including cases of species not deemed as threatened according to IUCN's assessments. Detailed studies at some particular regions are similarly alarming. For example, the annual magnitude of hunting in the Brazilian Amazon has been estimated in ~16 million mammals, or 23 million vertebrates in general.

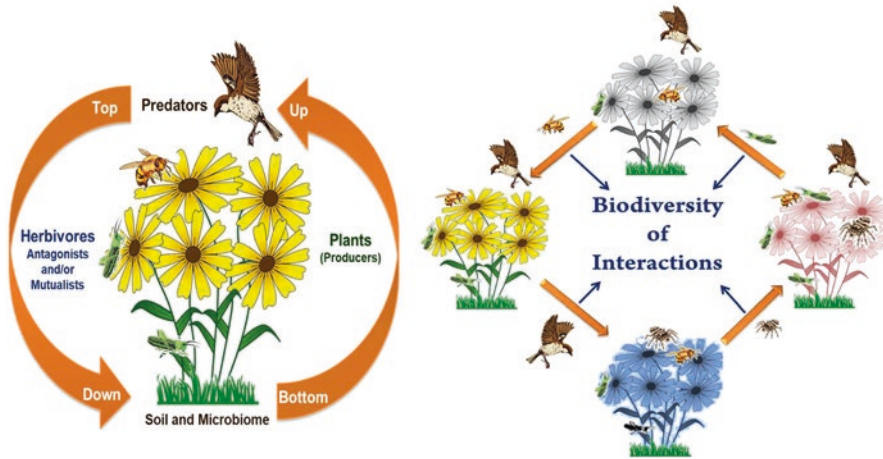
We know much less about the loss of invertebrates, mainly because we do not know the major part of this fauna, especially the cryptic below-ground species. However, according to Dirzo et al. (2014, and sources therein) 67% of monitored populations of invertebrates show ~45% mean abundance decline. More recently, a string of studies documenting declines in abundance of invertebrates have been published. While some of the papers report considerable declines (e.g. Wagner 2020). The most updated and thorough examination of data (166 long-term studies, encompassing 1676 sites), focusing on insects (van Klink et al. 2020) reports an average decline of 9%, much lower than that of the previous “Armageddon-type” studies (e.g., Sanchez-Mayo and Wyckhuys 2019), while also showing substantial heterogeneity across space (both within and among regions), biogeographic region, metric of abundance used, and time of measurement. Another salient aspect of this monumental work is the tremendous paucity of tropical studies – a critical knowledge lacuna for the understanding of plant-animal interactions in the Anthropocene.

Beyond the quantitative aspect of defaunation, an important emerging pattern is that, for vertebrates, susceptibility to anthropogenic impact is not random but instead varies with life-history traits, with an animal body size signal being particularly strong: medium and large animals are considerably impacted (“losers”) while small-bodied animals are frequently benefited (“winners”). A recent example in frugivorous birds and the associated plant species in the Atlantic forest of Brazil underscores this point (Emer et al. 2020).

What will be the impact of these human interferences in the structure of ecological networks that are based on plant-animal interactions? In this context, a broad, alarming issue is whether the Anthropocene may be a global forcing of a magnitude leading to mass, global disruptions of ecological interactions and potentially leading to the end of the biodiversity of interactions (sensu Thompson 2005, 2014)?

13.4 Contemporary Defaunation and the Consequences for Species Interactions

Biotic interactions are dynamic, and they vary in space and time. As was discussed in the introductory chapter, all types of such biotic interactions have existed for at least 300 million years. In the evolutionary process, species can be



■ **Fig. 13.3** A simplified multitrophic system (left) composed of plants, herbivores and herbivores' natural enemies. The elements of such a system do not live in isolation, however; rather they are immersed in a network of multiple species from each level. Such constellations of interacting species represent nodes in an ecological network with linkages between plants, animal consumers (invertebrates and vertebrates) and consumers' consumers within communities characterized by a rich diversity of interactions (right), maintaining viable natural communities. See also ► Chap. 10 of this book, Figs. 4 and 5, which illustrates a multitrophic system according to interspecific ecological networks involving plants and animals

replaced (i.e., extinction and speciation), yet independently of the existing species at any particular time, the interactions typically remain (Thompson 2005; Del-Claro et al. 2016). Through millions of years of evolutionary and coevolutionary processes, the interactions have shaped and maintained biodiversity (Thompson 2013). However, in the recent history of the Earth, critically over the last two centuries, one species has impacted nature in such a strong way that the evolutionary theater and its evolutionary plays, as we know them, are endangered (Dirzo et al. 2014).

In terrestrial environments, a simple trophic chain is composed of the plants, whose survival, growth and reproduction are directly dependent of abiotic forces such as climate, soil, and substrate, and intrinsic biotic factors such as their microbiome (see Reverchon and Méndez-Bravo, ► Chap. 8). The immediately next trophic level above plants is composed by its herbivores (invertebrates or vertebrates) and pathogens, which may also exert a strong negative pressure affecting plant fitness, in terms of survival, growth or reproduction, or several combinations thereof (see Marquis and Moura, ► Chap. 3). In contrast, other types of plant consumers play a positive role for plant performance, particularly via pollination or seed dispersal (see ■ Fig. 13.3; and see Figs. 4 and 5, in Luna and Dáttilo, ► Chap. 10 of this book). These animals are typically regarded as mutualistic interactors, since their positive role is generally rewarded by plant resources in the form of nectar, surplus pollen, or oils (for pollinators) and nutritious fruit (for dispersers). In addition, a number of plant species, encompassing a variety of lineages, interact with other consumers that serve as mutualists by affording anti-herbivore defenses to

the plant (Del-Claro et al. 2016, see also Moura et al., ► Chap. 5), which in turn provide rewards in the form of extra floral nectar, or lipids produced in specialized structures and, additionally, in a few cases, “housing” for the defenders (domatia). The interactions of plants with the antagonistic consumers (the herbivores) is regulated by (i) bottom-up factors consisting on intrinsic plant traits, such as secondary metabolites or nutritional characteristics, or the combination thereof, and (ii) the natural enemies of the herbivores, thus representing the top-down regulating factors. Such top-down forces, predators or parasitoids, can control the abundance and diversity of herbivores (■ Fig. 13.3). However, these interactions are much more nuanced and non-linear than this description suggests, as plants and their consumers, and the consumers’ consumers do not live in a vacuum. For example, a bee species rarely is a specific pollinator of just one plant species; frequently it is the pollinator of several plant species (see Torezan-Silingardi et al., ► Chap. 6). Likewise, although some herbivores can be specialized on a host plant, many herbivores are generalists to some degree, polyphagous animals that feed on different plant species; and plants in turn can be the food source of one or multiple herbivores. Feeding on distinct plants and moving among different areas and populations, frugivores can disperse seeds and improve plant variability through genetic recombination (see Holeski, ► Chap. 7). Animal predators specialized in one or few prey items are not the general rule. So, each one of these plant-animal multitrophic systems are not isolated in single communities. Herbivores, microorganisms, predators, parasites, and facilitators, ultimately represent a large amount of nodes connected by links across different multitrophic systems (■ Fig. 13.3). Considering a given community, one can envisage the complexity of the networks, even in the case, of, for example, two trophic levels, such as the plants in a community, and its links to their pollinators and their herbivores—hybrid networks. For example, Morrison et al. (2020) has constructed a network of plants and the associated communities of herbivores and pollinators, in a relatively simple temperate community. These connections between nodes of ecological networks structure the biodiversity of interactions, the multitude of different connections among species that maintain the viability and functionality of natural communities (Thompson 2005, 2013, 2014).

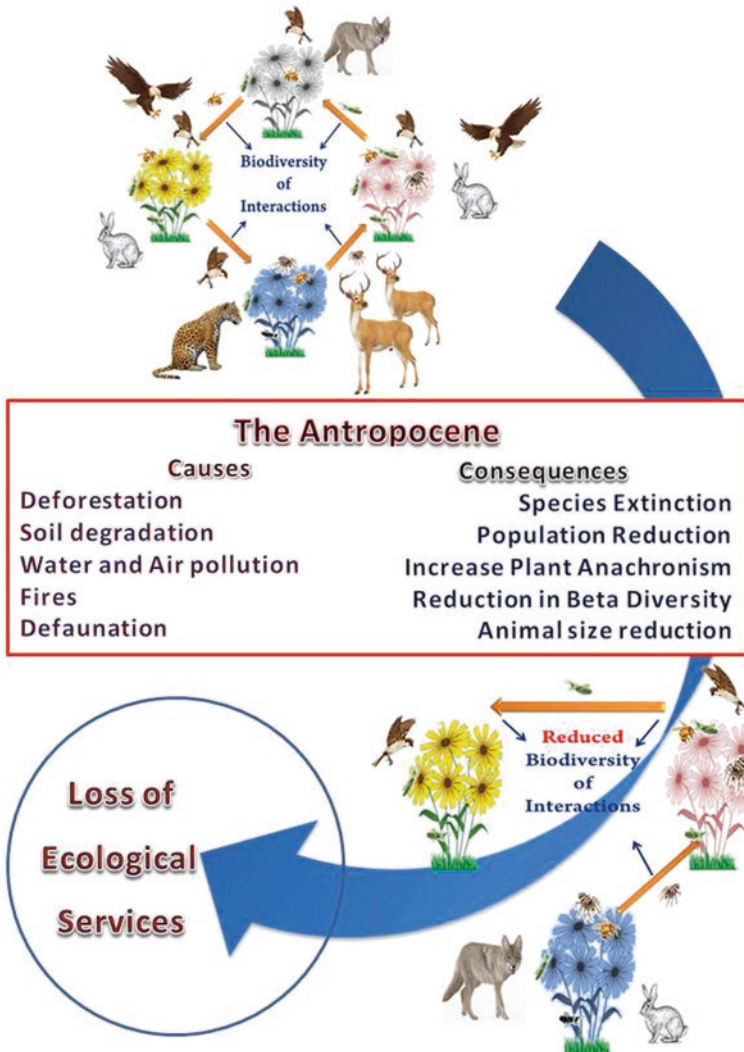
Studies of plant-animal interactions in light of contemporary defaunation have focused largely on mutualistic interactions (pollination, seed dispersal), while those examining antagonistic interactions of herbivory and seed predation remain appallingly under-represented in the literature (e.g. Gardner et al. 2019). However, the few available suggest that the richness of this sort of plant-animal interactions can also be dramatically affected. In one particular example in Mexican tropical forests, researches have shown that contemporary defaunation of the understory herbivores can actually lead to the local extinction of mammalian herbivory: a large sample of carefully monitored plants over multiple years, showed that in contrast to intact sites, plants in a heavily defaunated forest showed consistent absence of herbivore damage (Dirzo and Miranda 1990, Dirzo et al. 2020). The consistent absence of foliage herbivory led authors of this work to suggest that this represents a case of the local extinction of a plant-animal interaction.

The seminal coevolution paper by Ehrlich and Raven (1964) advocated that plant-animal interactions have played an essential role in the generation of Earth's biodiversity. Bascompte and Jordano (2007) extended this view pointing out that mutually beneficial interactions between plants and pollinators and seed dispersers have been paramount in the generation of Earth's biodiversity (see Bronstein, ► Chap. 11). These mutualistic interactions often involve dozens or even hundreds of species that form complex networks of interdependences, whose structure has important implications for the coexistence and stability of species as well as for the coevolutionary process (Bascompte and Jordano 2007). We know that more than 90% of tropical plant species rely on animals for the dispersal of their seeds (Jordano 2000), and similar numbers are reported for pollination interactions (Bawa 1990). In addition, in the food chain of higher plants, herbivorous insects and their natural enemies, comprise a significant fraction of Earth's known species richness (just shy of 80%) engaged in herbivory (Dirzo et al. 2020). If these animals disappear, their plant partners may follow suit and, likely, the associated microbiome too (see Reverchon and Méndez-Bravo, ► Chap. 8).

Obviously, the pulse of "Anthropocene defaunation" described above has cascading effects that will affect all organisms and ecosystems across the planet's ecosystems, impacting directly plants via herbivory, pollination and dispersal. But it also affects human health and economy, considering the enormous loss of ecological services (mainly pollination; see Torezan-Silingardi et al. ► Chap. 6). Defaunation, including local, regional or the complete extinction of vertebrates and invertebrates species, will disrupt uncountable plant-animal interactions, with direct effects in energy flow through communities and also gene flow, possibly producing new evolutionary pathways. The local or regional biodiversity of interactions will have to be rebuilt, if possible. Gardner et al. (2019) conducted a meta-analysis pointing out that real-world defaunation caused by hunting and habitat fragmentation leads to reduced forest regeneration. The elimination of seed dispersers and frugivores like primates and birds, may cause the greatest declines in forest regeneration, with impacts on carbon stores and climate change.

Defaunation precipitates the extinction of evolutionarily distinct interactions, as clearly demonstrated by Emer et al. (2020) in an elegant study with frugivorous birds and its associated plant species. These authors suggested that defaunation is driving evolution to the reduction in the size of seeds and dispersers. Additionally, they demonstrated that defaunation is provoking the loss of interactions involving unique lineages of bird and plant species. A direct result of this contemporary human-driven disturbance is the loss of an irreplaceable set of genetic variability.

Biodiversity is not a product of single interactions that occur in a determined place and time. On the contrary, it is a dynamic result of uncountable relationships, with extremely conditional outcomes and variable according to the mosaic of species present in the environment. In the network of ecological interactions that maintain viable natural communities, the beta diversity or the diversity of connected species among local and regional populations is the best indicator of the health of a natural system (e.g. Dáttilo and Rico-Gray 2018). In this scenario animals are the connectors per excellence, the mobile force of beta diversity in plant-animal ecological networks. Thus the human-driven negative impacts on nature,



■ **Fig. 13.4** The Anthropocene is producing strong negative impacts on nature, including deforestation, soil degradation (with loss of soil microbiomes), water and air pollution, and uncontrolled hunting and fires leading many ecosystems to a status of defaunation. The loss of animal links in the ecological networks (upper panel) due to extinction and population reduction cause the loss of connections (beta diversity) within and between communities (lower panel). Entire trophic chains and connections between distinct networks are being lost causing a severe reduction of biodiversity of interactions and of ecological services

resulting in defaunation, are indeed breaking the links between nodes of ecological networks so rapidly that it is unlikely that nature will have time to replace the actors of the evolutionary plays (e.g. Thompson 2005, 2013, 2014, ■ Fig. 13.4).

Conclusion

Plant-animal interactions are dynamic, and they vary in space and time. The biodiversity of interactions they originated through evolutionary time is one of the main drivers of diversification and success of life on Earth. Anthropocene defaunation, accelerated since the last century, is producing disruptions in the diversity of interactions and ecological networks. Animals are declining in numbers, losing populations, and changing in size-distributions, which causes degradation of ecological services. The natural dynamics of speciation and extinction maintains, over time, constellations of interacting species. However, in the Anthropocene, defaunation is occurring at such a rapid pace and globally, that it begs the question: will we maintain and or have time to restore the constellations of species interaction networks that sustain humanity?

Key Points

1. Defaunation and its impacts in plant-animal interactions is omnipresent in the Anthropocene;
2. Deforestation, defaunation, fires, and pollution, have negative impacts on the biodiversity of interactions;
3. Defaunation disrupts species interactions and plant-animal networks;
4. Defaunation-related degradation of species interactions has cascading consequences of significance for human wellbeing

Questions

1. How does defaunation impact plant-animal interactions and biodiversity as a whole?
2. Are defaunation and deforestation accelerated in the Anthropocene as a result of humanity's negative impacts in the natural environment?
3. Discuss with your classmates or colleagues, what actions we could take to reverse or stop defaunation. Elaborate three viable suggestions.

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