

# The Long Arm of Species Loss: How Will Defaunation Disrupt Ecosystems Down to the Microbial Scale?

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*As the world's sixth mass extinction continues, the loss of large animals has widespread effects on biodiversity and ecosystem processes. Research across disparate systems, such as grasslands, marshes, forests, and coral reefs, shows that the effects of defaunation manifest even at the microbial scale, affecting microbial communities, microbe-driven processes, and host–microbe interactions. Microbiomes of foundation species, such as corals, trees, and grasses, appear especially vulnerable to the loss of large consumers, often resulting in disease, mortality, and regime shifts in ecosystems. We use the concepts of cascading consumer–prey interactions, as well as the bottom-up roles of consumers in ecosystems, to outline how future research can fill gaps in the field. For example, consumer diversity and body size affect the strength of trophic cascades and likely shape how defaunation affects microbiomes. Ultimately, we argue that the connections between macrobes and microbes are likely common but underappreciated, as the impacts of losing large consumers radiate throughout ecosystems.*

*Keywords: microbiome, trophic cascades, overkill, ecosystem function, bottom-up*

**T**igers or termites? Blue whales or bacteria? Fishes or fungi? Big and rare or little and abundant? Which kind of organisms matter most to ecosystems—hairy, four-legged beasts or little bugs? Three decades ago, two pillars of ecology, Edward O. Wilson and John Terborgh, argued that very point. Wilson, famous for his pioneering work on the sociobiology of ants, argued that “It is a common misconception that vertebrates are the movers and shakers of the world” (Wilson 1987). Instead, he proposed that the “little things,” such as insects, run the show. Wilson was specifically arguing for invertebrates, such as ants and termites, because of their spectacular diversity and impact on community dynamics and ecosystem processes.

While Terborgh did not dispute the importance of Wilson’s “little things,” he was partial to the “big things that run the world” (Terborgh 1988). Terborgh, studying faunal collapse in the Neotropics, argued that the loss of large, rare animals, such as jaguar, harpy eagles, and peccaries, had much farther-reaching effects on ecosystem dynamics. He and others found that the loss of these megafauna via over-exploitation or habitat loss resulted in declines of important forest fauna and drastic changes in the seed recruitment of tropical plants, which, together, altered the diversity and

function of tropical forests. Therefore, the loss of these large animals, Terborgh argued, “would work to the detriment of many of Professor Wilson’s ‘little things’” (Terborgh 1988).

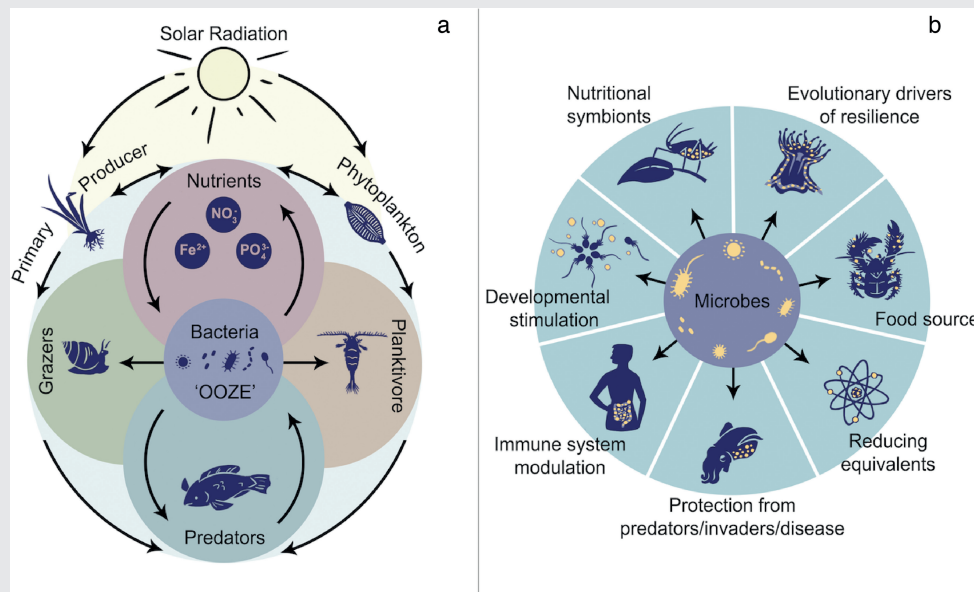
Clearly, both Wilson and Terborgh were right; both large and small organisms drive various aspects of community dynamics and ecosystem function, often in complex, interactive, and sometimes unpredictable ways. But one major group of organisms, the microscopic members of the communities, were all but ignored at the time Wilson and Terborgh’s debate played out. Since their dueling articles, advances in culturing techniques and molecular biology have allowed microbiologists to more clearly view the vast abundance and diversity of the “unseen microbial majority” (reviewed in Rappé and Giovannoni 2003). Microbes are in many cases the dominant, albeit morphologically smallest, players in ecosystem function and are often crucial to the health and function of their hosts (see box 1). Microbes mediate a myriad of processes, including species range limits, disease dynamics, and global biogeochemical cycling (for a review, see Bertrand et al. 2015). Similarly, macroscopic organisms fundamentally shape nutrient distribution, primary production, and species diversity (Estes et al. 2011). However, most research to date had been focused on the

**Box 1. Host–microbe services in the age of defaunation.**

Up until the 1940s, most ecologists studying large, multicellular organisms grouped all microorganisms into mysterious black boxes. For example, in a now famous figure, Lindeman (1942) placed bacteria and ooze at the center of a lake food web. He suggested that microorganisms were clearly at the center of ecosystem processes, although their true taxonomic identities, numbers, and metabolic potentials were mostly a mystery (figure 1a). Now, we appreciate the complicated influences that diverse bacteria, archaea, protists, and fungi have on their macroscopic hosts (for reviews, see McFall-Ngai et al. 2013, Russell et al. 2014), ecosystem processes (Bell et al. 2005, Delgado-Baquerizo et al. 2016), and ecosystem services (McKenney et al. 2018). Microbes provide numerous services to their hosts such as provisioning essential sources of micronutrients, amino acids, and lipids, as well as antimicrobial production (Raina et al. 2016) and immune system modulation (Chu and Mazmanian 2013; figure 1b). These new concepts in microbial ecology and symbiosis have affected how we view macroscopic community ecology and led to formation of entirely new fields focused on host-associated and even ecosystem-associated microbiomes.

Given that losses of large consumers shift microbiome diversity, structure, and stability, it is also likely the disappearance of these animals also affects host–microbe services. For example, following the loss of herbivorous fishes, competition with algae changes the functional roles of the coral microbiome and alters important microbial–host services. In corals exposed to algal competition, there was a decline in bacterial metabolic pathways for photosynthesis, amino acid synthesis, and antibiotic production, and an increase in metabolic pathways associated with opportunism and virulence, such as bacterial invasion systems, bacterial motility, and secretion systems (Zaneveld et al. 2016). Losses of herbivorous fishes and the rise of algal competition not only reorganized the taxa in the coral microbiome but also compromised the host services that the microbiome provides and ultimately led to coral death. Likewise, in grasslands, declines in ungulate herbivory reduce the abundance of fungal endophytes in grasses, which potentially alters the ability of grasses to withstand herbivory and drought (Rudgers et al. 2016). Therefore, the abundance of large consumers appears to have important sway over key host–microbe mutualisms that influence ecosystem function, although this avenue of research needs further development.

Another relatively unexplored aspect of how large consumers affect host–microbiome interactions is how alteration of predator abundance could affect the host microbiomes of their prey. Predation risk is a significant source of stress for prey populations that manifests in changes in physiology as well as declines in reproduction (Hawlena and Schmitz 2010). In humans, stress affects the microbiome, especially in the gut, and likely also affects host services the microbiome provides (Galley et al. 2014, Zaneveld et al. 2017). Therefore, by extension, the stress that predation risk exerts on prey populations may also cascade to affect prey host–microbiome relationships that, in turn, influence prey health. The links between defaunation and host–microbiome interactions should be a fruitful new area of developing research.



**Figure 1. Changing views of the roles of microbes in ecosystems. (a) Historically, studies of community and ecosystem ecology have viewed bacteria and other microorganisms as primarily black boxes that function exclusively as a food source to form the bottom of most food webs, such as those found in lakes as was shown in Lindeman (1942). Trophic guilds, such as grazers and planktivores, consume this bacterial ooze in addition to other primary resources such as plants and phytoplankton that are stimulated by the presence of necessary nutrients, such as nitrogen (e.g., NO<sub>3</sub><sup>-</sup>), phosphorus (PO<sub>4</sub><sup>3-</sup>), and iron (Fe<sup>2+</sup>). (b) However, since the middle of the twentieth century, our understanding of the role of microbes (i.e., bacteria, archaea, viruses, and microeukaryotes) has dramatically expanded to include aspects of animal ecology outside the realm of food webs, including protection from predators, immune system modulation, and resistance to environmental stress among other functions.**

ecology of only one end of this size spectrum—*Escherichia coli* or elephants, *Wolbachia* or whales—with fewer studies integrating these vastly different biological scales.

In the present article, we explore how the loss of macrofauna species, or defaunation, in the Anthropocene (Dirzo et al. 2014, McCauley et al. 2015) will likely influence the abundance and diversity of microbes, as well as the functional roles of those microbes across different ecosystems. The study of the widespread effects of animal losses is not new by any regard (Terborgh and Estes 2010). Rather, the goal of this perspective is to highlight recent work that connects the loss of large consumers to microbial community dynamics, host microbiomes, and previously unrecognized microbe-driven feedback loops that contribute to ecosystem decline. Given that this is an emerging area of research, providing an exhaustive literature review and synthesis is not feasible. Instead, our goal is to highlight emerging themes across disparate ecosystems of how the loss of large animals disrupts ecosystems down to the microbial scale, often compromising the health of foundation species and affecting key ecosystem processes. We hope to encourage ecologists and microbiologists to collaboratively embrace fruitful new avenues of research that are focused on complex connections between the ecology of macrobes and microbes in this era of rapid defaunation.

### How does defaunation affect microbiomes?

Predators and herbivores are critical to ecosystem function. Their loss affects a host of community properties and ecosystem processes, such as competition, species diversity, organismal biomass, primary productivity, and nutrient cycling (Estes et al. 2011, Doughty et al. 2016, Zhou et al. 2017). More recently, widespread declines in smaller animals (e.g., bees and other pollinators) emphasize the outsized effect of these smaller but still macroscopic creatures on ecosystem processes and ecosystem services (Potts et al. 2010). The rapid loss of many of these crucial species has affected the function of many ecosystems worldwide (Dirzo et al. 2014), even altering microbe-driven processes (Schindler et al. 1997). Below, we outline three systems with dynamic links between defaunation and alterations in microbiomes that have strong consequences for ecosystem function.

**Herbivorous ungulates drive plant community dynamics and soil microbiome diversity in grasslands.** In terrestrial ecosystems, large herbivores strongly affect aboveground primary production and biodiversity (Koerner et al. 2018). In addition, herbivory can have significant impacts on biogeochemistry and biodiversity below ground by affecting both soil microbes and soil nutrient cycling (Zhou et al. 2017, Ritzenthaler et al. 2018). Although there is significant context dependency in the impact of herbivores on soil microbes that depends on system productivity, grazing intensity, plant palatability (Bardgett and Wardle 2003, Zhou et al. 2017), most work in this area has been focused on how herbivore loss affects microbial abundance and microbe-driven processes. For

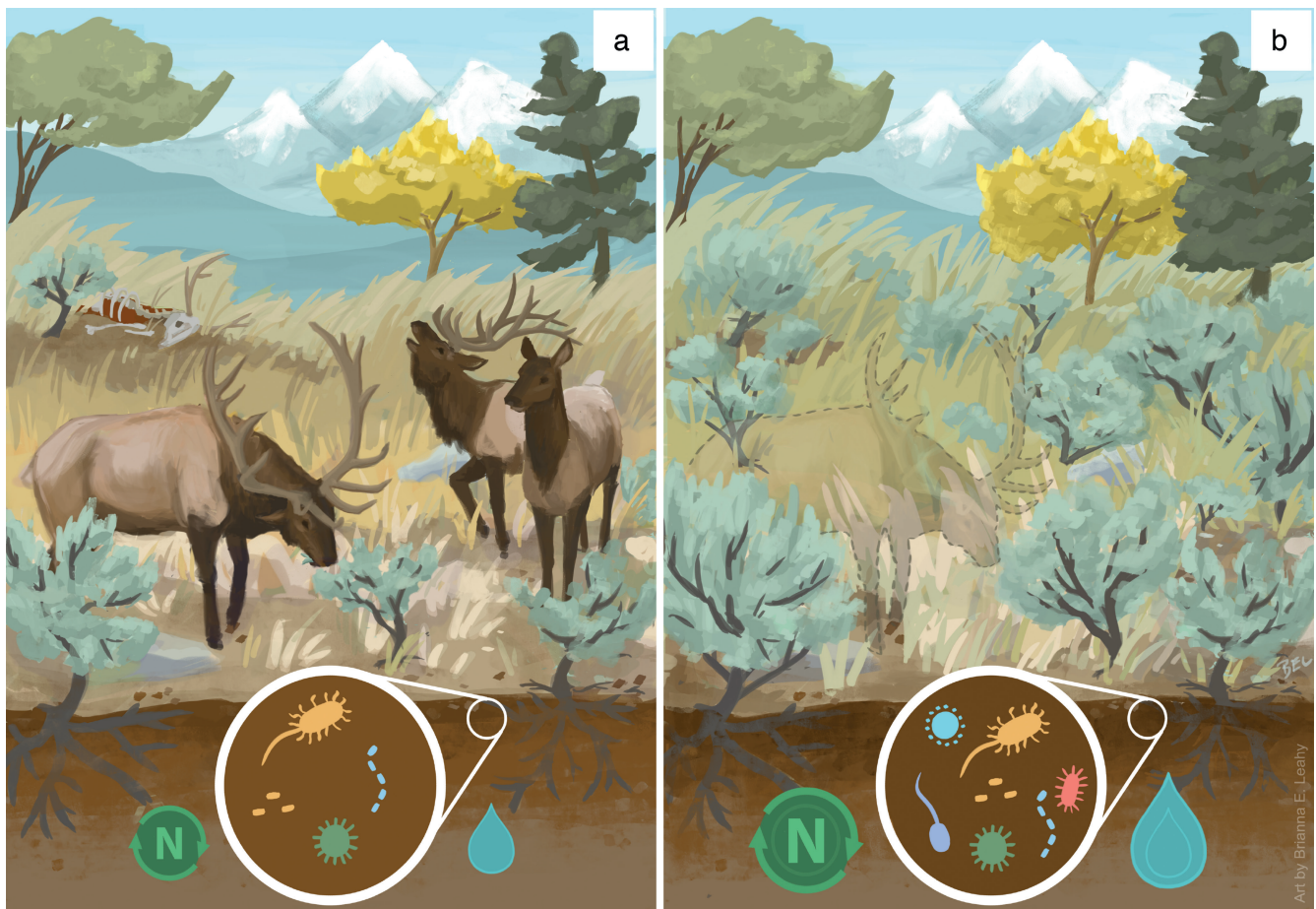
example, the exclusion of African ungulates led to a 25% increase in soil fungi (Sankaran and Augustine 2004), and grazing by herds of zebra, wildebeest, and other antelopes increased rates of soil nitrogen cycling (McNaughton et al. 1997). Similarly, bison grazing in Yellowstone National Park increased nitrogen cycling by microbes but did not affect soil microbial biomass (Tracy and Frank 1998). Together, these studies suggest that large herbivores are a strong determinant of microbial abundance and biogeochemistry, but their impacts on microbial diversity and community dynamics have received much less attention.

In a recent study excluding North American elk from winter foraging areas, soil microbial abundance and activity were analyzed, as were the microbial biodiversity changes that occur when herbivores are lost. The removal of elk altered the abundance, diversity, and function of soil microbial communities that coincided with significant increases in shrub abundance and leaf litter accumulation, as well as soil water content (Cline et al. 2017; figure 2). As shrub abundance increased and more leaf litter accumulated on the ground following elk removal, bacterial richness also increased. The beta diversity of bacteria and fungi also increased, meaning that the microbial communities became more variable when the elk were removed. These altered microbial communities, in the absence of elk, led to increases in microbial enzyme activity in the soil, especially for enzymes that breakdown cellulose, likely as a result of the increased leaf litter following the increase in shrubs released from elk browsing.

Furthermore, because the differences in microbial beta diversity increased between areas with and without elk, the difference in microbial genes involved in carbon and nitrogen cycling also increased (Cline et al. 2017). This functional difference was likely responsible for the 50% increase in microbial respiration rates and 70% increase in nitrogen mineralization rates in the areas without elk (Peschel et al. 2015). Together, these data suggest that losing herbivores not only affects aboveground biodiversity but cascades down to affect the composition, activity, stability, and function of soil microbiomes. These shifts in microbial function ultimately feed back on the soil chemistry, resulting in changes in the aboveground communities as a result. Future research could take advantage of ongoing herbivore exclusion experiments worldwide (e.g., Borer et al. 2014, Koerner et al. 2018) to ask key questions about how contexts such as productivity, plant diversity, and soil type affect the links between herbivores and soil microbiomes.

**Trophic cascades, fungal-farming invertebrates, and the collapse of foundation species.** Although large herbivores exert cascading effects on microbial diversity in grasslands, both predators and herbivores exert strong control over microbial dynamics in salt marsh ecosystems. An excellent example is herbivory by the marsh snail, *Littoraria irrorata*, which controls the abundance of *Spartina alterniflora*, the dominant marsh plant and an important foundation species in the marshes of



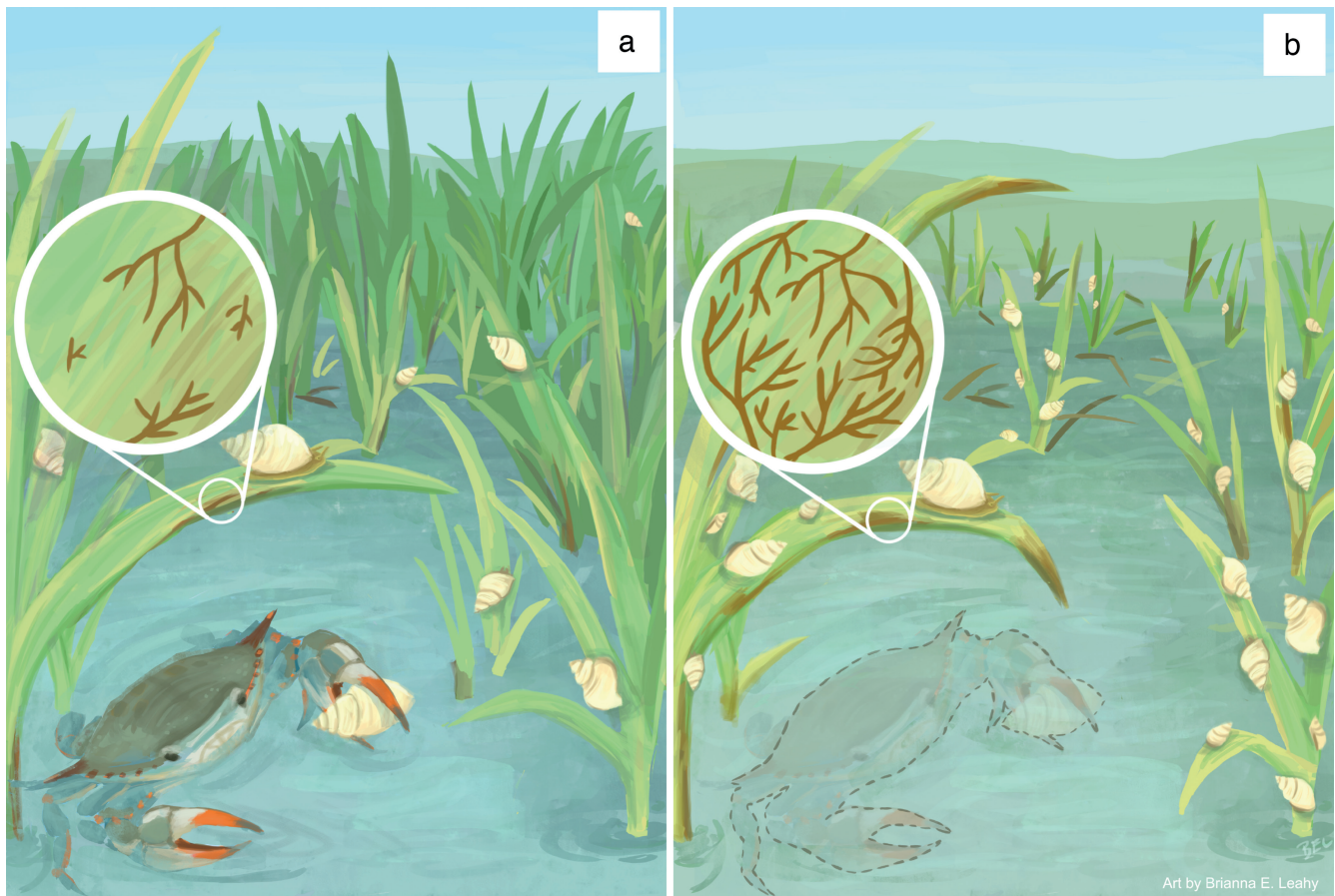


**Figure 2.** Herbivory by elk alter aboveground ecology and below ground microbiology and biogeochemical cycling. (a) American elk (*Cervus elaphus*) suppress shrub abundance and help reinforce grass-dominated communities. (b) Exclusion of elk (notice the “ghost” elk presence) increases shrub abundance. In addition, soil water content also increased (compare the size of water droplets across panels) along with the abundance, diversity and function of soil microbial communities (compare the microbes in the magnifying glass), which resulted in increased nitrogen mineralization rates (notice the larger N in panel (b) denoting more nitrogen and the larger arrows denoting faster cycling). Surprisingly, elk exclusion also altered bacterial richness and beta diversity of both bacteria and fungi, with bacterial respiration rates increasing in areas in which elk were absent. Therefore, these ungulates exert strong top-down controls on plant communities, abiotic soil properties, and microbial diversity that shape rates of nutrient mineralization. See Peschel and colleagues (2015) and Cline and colleagues (2017) for details.

the southeastern United States (Silliman and Zieman 2001). There is a strong trophic cascade in this system in which predation by terrapins, fishes, and especially blue crabs (*Callinectes sapidus*) controls the abundance of marsh snails and thereby reduces their grazing impacts on *Spartina* (figure 3a). Overharvest of these predators leads to increased consumption of marsh grasses by snails and the denuding of areas of salt marsh (Silliman and Bertness 2002).

However, the major impact of marsh snails on *Spartina* is surprisingly not from direct consumption of the grasses but from the farming of microscopic fungi within the marsh plants (Silliman and Newell 2003). These fungi are always present on the marsh grasses as part of their normal microbiome, although their role in the microbiome is currently

unknown. The *Littoraria* snails scrape small wounds on the surface of the marsh grass to cultivate the fungi by depositing fecal material into the wound that enhances fungal growth within the plant tissues (figure 3b). The snails then preferentially feed on the fungal biomass rather than consuming the live plant tissue. The combined effect of snails and fungal growth together decreases the growth of marsh grasses, with the fungal infection alone resulting in a reduction of up to 60% in growth (Silliman and Newell 2003). Therefore, by keeping snail populations low, larger predators mitigate the negative effects of this fungal disruption in marsh grasses. The disruption of these predator–prey interactions leads to a microbe-mediated cascade that, when combined with climate change–associated drought, has driven the widespread



**Figure 3. Exploitation of top predators results in increased snail-mediated fungal infections and loss of marsh grasses.** (a) In intact salt marsh communities, blue crabs (*Callinectes sapidus*) and other predators prey on herbivorous snails (*Littoraria irrorata*). These snails typically consume the dominant marsh grass (*Spartina alterniflora*) and the fungi that they farm on the leaves of the marsh grass. (b) Overharvesting of crabs and other snail predators (notice the “ghost” of crab predation past) leads to an increase in snail abundance, which results in suppression of marsh grass. Interestingly, much of the suppression of marsh grass in the presence of abundant snails comes from increased growth of fungi on and in marsh grasses (notice the increase in fungal hyphae in the magnifying glass in panel (b)). Therefore, the loss of predators leads to abundant snails facilitating fungal infections in the marsh grass that then leads to grass decline. For details, see Silliman and Zieman (2001), Silliman and Bertness (2002), Silliman and Newell (2003), and Silliman and colleagues (2005).

decline of salt marshes across the southeastern United States (Silliman et al. 2005). The impact of consumers on the disruption of marsh plant microbiomes and on their decline appears to be general to different types of herbivores and plants (Daleo et al. 2009, Daleo et al. 2018), suggesting these interactions may be underappreciated in scope and scale.

Importantly this trophic cascade-induced but microbe-mediated collapse of a foundation species is likely not limited to marsh grass systems. Fungal farming is common across many groups of terrestrial insects, including ants, termites, and beetles (Mueller and Gerardo 2002). For example, many species of bark beetles (Coleoptera: Curculionidae: Scolytinae) colonize conifer trees by making holes in their subcortical tissue (Paine et al. 1997, Raffa et al. 2015). These beetles then infect the tree with fungi that are typically specialized symbionts of the beetles. The invasive fungi disrupt

the microbiome of the conifers, concentrating nitrogen from the tree sap and forming the majority of the beetles' diet (Raffa et al. 2015). Although low levels of bark beetle colonization may have a minimal impact on the health of trees, large infestations can kill whole stands of conifers containing thousands of trees. These infestations and the resulting widespread tree mortality are increasingly common, resulting in significant ecological and economic costs (Raffa et al. 2008).

Like the snail–fungus–marsh grass example, predators likely affect the beetle–fungus–tree cascade. Woodpeckers, beetles, flies, and numerous parasitoid arthropods are all important predators of bark beetles (Wegensteiner et al. 2015). In particular, woodpeckers can consume up to 98% of available bark beetle larvae and strongly limit populations of bark beetles in pre-epidemic phases (Fayt et al. 2005). The



loss of key woodpecker habitat or habitat fragmentation may release bark beetles from strong top-down control and facilitate beetle outbreaks that ultimately lead to fungus-mediated tree mortality (Fayt et al. 2005). Climate change may also be an important driver of bark beetle populations by increasing the stress on trees, reducing their defenses against beetles, and making them more susceptible to infestations and fungal infections. Therefore, there could be significant interactions between climate forcing and declines in predators in controlling beetle outbreaks and fungus-induced tree mortality (Raffa et al. 2008), similar to the snail–fungus–marsh grass cascade (Silliman et al. 2005).

**Overfishing and the microbialization of coral reefs.** Overfishing is one of the primary contributors to the degradation of coral reefs worldwide. Losing carnivorous and herbivorous fishes from reefs increases the abundance and diversity of macroalgae, increases adult coral mortality, and decreases the recruitment of juvenile corals (Sandin et al. 2010). At the same time, removing these higher-order consumers fundamentally alters microbial dynamics both on corals and in the water surrounding reefs. For example, ecological and metagenomic comparisons across large geographic regions showed that reefs with fewer carnivorous and herbivorous fishes contain fewer corals, more algae, and starkly different microbial communities (Dinsdale et al. 2008, Sandin et al. 2008). Although the dominant flow of energy is toward higher trophic levels (i.e., predators and herbivores) on many near-pristine reefs, energy is shunted on overfished reefs toward the base of the food web—toward the microbes (McDole et al. 2012).

This microbialization of human-affected reefs strongly correlates with low abundance of corals and high abundance of fleshy algae on reefs (Haas et al. 2016). Much like excluding ungulates from a grassland, removing herbivores from areas of reef leads to rapid increases in abundance and diversity of benthic algae and a decline in corals (Hughes et al. 2007, Burkepille and Hay 2008). Algae can outcompete corals for space via a variety of mechanisms, one of which is the disruption of coral microbiomes that leads to reduced coral growth and potentially disease (Vega Thurber et al. 2012). Therefore, one of the hypothesized drivers behind the microbialization of coral reefs is that the loss of large consumers leads to more algae, increasing competition between algae and corals and altering the dynamics of coral microbiomes.

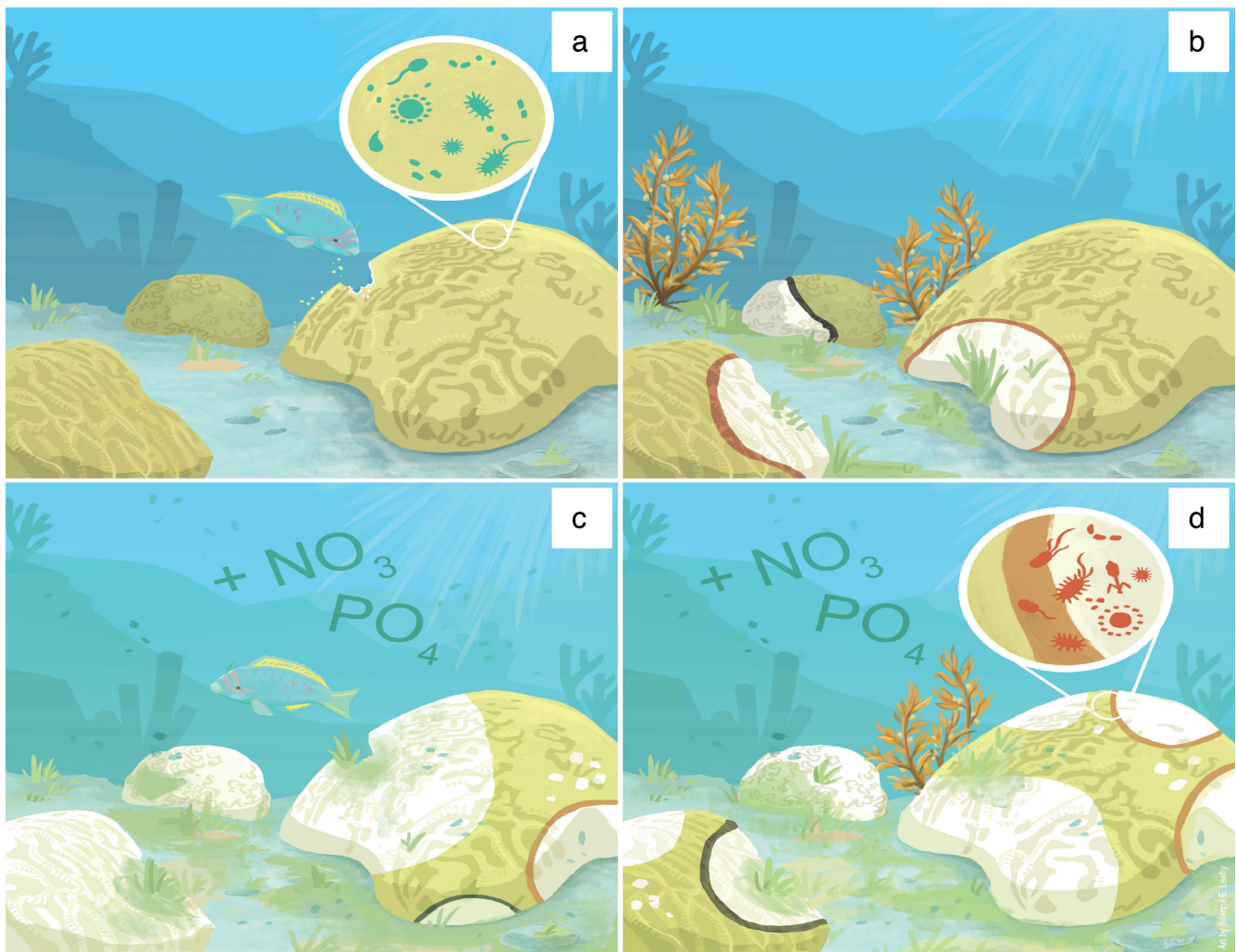
For example, the experimental removal of herbivorous fishes on a reef caused significant increases in algal abundance, more intense coral–algae competition, and shifts in the composition and variability of the coral microbiome, which were linked to increases in coral disease and mortality (Zaneveld et al. 2016). Competition with algae not only disrupted the taxonomic diversity of microbes on corals and increased the variability (beta diversity) of the coral microbiomes, but it also changed the functional roles of the coral microbiome. In corals exposed to algal

competition, there was a decline in bacterial metabolic pathways that are positively correlated with coral health, such as photosynthesis, amino acid synthesis, and antibiotic production, and an increase in metabolic pathways associated with opportunism and virulence, such as bacterial invasion systems, chemotaxis, and bacterial motility (Zaneveld et al. 2016). Therefore, losses of herbivorous fishes and the resulting rise of algal competition not only reorganized the taxa in the coral microbiome but also compromised the key host services that the microbiome provides (see box 1), ultimately leading to the death of corals (figure 4a, 4b).

However, large consumers need not even be lost for their impact on microbiomes to radically change. For example, predation on corals by fishes such as parrotfishes is often not life threatening to most corals (Bonaldo et al. 2014). However, changes to abiotic conditions may fundamentally alter this interaction. Under nutrient enriched conditions, corals bitten by parrotfish lost tissue and died 66% of the time, compared with 0% mortality of corals bitten under ambient nutrient conditions (Zaneveld et al. 2016). The increase in mortality was linked to increases in potentially pathogenic bacteria on the surface of the bitten corals in nutrient rich areas (compare figure 4a, 4c). Therefore, this unexpected and worrisome observation shows that nutrient pollution turns parrotfish, which are normally thought of as coral allies, into agents of mortality for some corals. Most importantly, this work suggests that alterations to abiotic forcing can fundamentally change interactions between consumers and microbes, with potentially dramatic repercussions for both host–microbiome interactions and ecosystem function.

### Patterns arising in how the defaunation of ecosystems disrupts microbiomes

Unfortunately, too few studies exist to generate a meaningful synthesis of how defaunation affects microbial communities. This paucity of data is, in part, why we wrote this perspective. Because many of these interactions are similar to classic questions in the ecology of consumer–prey interactions, important questions about what processes modify the strength and extent of consumer–prey interactions make a meaningful scaffold for thinking about how the impact of defaunation could affect microbial communities. For example, the length of food chains, consumer body size, and consumer metabolism are all strong determinants of how predator loss ripples throughout an ecosystem (i.e., a trophic cascade; Borer et al. 2005, Shurin and Seabloom 2005). Furthermore, the diversity of consumers—both herbivores and predators—often determines how strongly consumer–prey interactions affect community dynamics and ecosystem function (Duffy et al. 2007). Below, we outline several important questions about how these classic questions in consumer–prey ecology could shape future research on the cascading effects of defaunation on microbial communities and processes.



**Figure 4.** Top-down and bottom-up factors interact to change the microbial communities on corals, leading to decline of reef habitats. (a) On healthy coral reefs, parrotfishes and other herbivorous fishes are generally considered allies of corals because they consume large amounts of algae that otherwise compete against corals for space. (b) Overfishing of these herbivores leads to increases in the abundance and diversity of algae, ultimately leading to changes in the coral microbiome, increases in coral disease and reductions in coral growth and increases in coral mortality (notice the dark disease margins and dead white coral tissue). (c) While under normal conditions, occasional coral predation by parrotfishes occurs is generally benign (notice bites from coral in panel a), with increased nutrient pollution, this trophic interaction turns deadly and a majority of corals bitten by these fishes die as the combination of predation and nutrient pollution dramatically change the coral microbiome. (d) The combination of overfishing and nutrient pollution often works synergistically to alter the coral microbiome and further reduce coral reef health (notice the magnifying glass denoting dramatic change in coral microbial communities as compared to healthy corals in panel (a)). See Vega Thurber and colleagues (2012) and Zaneveld and colleagues (2016) for details.

**How often do trophic cascades trickle down to affect microbial communities?** A classic question in consumer–prey ecology is how much the ecological effects of predators are transmitted to lower levels of a food web, or how much these cascades trickle down to primary producers (Halaj and Wise 2001, Shurin et al. 2002). Because alterations in herbivore abundance and their impacts on primary producers appear to be a major signal in affecting microbial communities (ungulates, shrubs, and soils; parrotfishes, algae, and corals), it

may be that the major effect of defaunation on microbiomes comes from the alteration in herbivore abundance. Are predators too far removed in food webs to affect microbial communities and their ecosystem processes?

Whole-lake experiments have been key to exploring trophic cascades (Carpenter et al. 2010) and have started to reveal how predators influence microbiomes. In a recent study, not only did the addition of fishes to a lake reduce herbivorous zooplankton abundance, but it also led to

significant changes in the composition of the lake's microbial community (Devlin et al. 2015, Saarenheimo et al. 2016). The abundance of methanotrophs (i.e., bacteria that consume methane) increased significantly, resulting in a tenfold reduction in methane emissions from lakes with fishes (Devlin et al. 2015). Given that methane is a greenhouse gas 25 times more potent than carbon dioxide, the loss of fishes in similar lakes may have significant unexpected effects on climate forcing. Mesocosm experiments also show similar patterns to whole-lake experiments in which the presence of predatory fishes alters both bacterial abundance and composition (Sullam et al. 2017) and also the metabolic processes for how bacteria degrade, uptake, and use dissolved organic carbon (Limberger et al. 2018). These impacts of predators on microbial dynamics are somewhat surprising, given that microbes in similar aquatic systems are often assumed to be controlled from the bottom up by energy and nutrient limitation rather than from the top down by trophic interactions (e.g., Elser et al. 1995).

There are multiple nonexclusive mechanisms of how predators could affect microbial community structure and ecosystem level processes. First, predators could indirectly affect microbiomes via their effects on absolute herbivore abundance that cascades to primary producers, soils or water, and their associated microbes. This impact is clear from fungus-induced salt marsh decline following removal of predatory crabs and fishes (Silliman and Newell 2003) and from whole lake experiments in which fishes suppress herbivorous zooplankton (Devlin et al. 2015, Saarenheimo et al. 2016). Second, predators could affect microbiomes via their effect on herbivore behavior, in which predation risk can create a landscape of fear that shapes herbivore foraging, and via their effects on primary producer communities. Although a robust literature exists on how predation risk affects herbivore behavior and herbivory (for reviews, see Schmitz 2005, Laundré et al. 2010, Burkepile and Parker 2017), it is less clear that the impact of predation risk cascades down to affecting microbiomes. However, evidence from some terrestrial systems suggest that predation risk can drive spatial differences in nitrogen mineralization in soils because of altering herbivore space use (Frank 2008) and that predation risk can alter the stoichiometry of prey species, which changes how prey carcasses decompose in the soil (Hawlena et al. 2012). Because microbes drive soil processes, these studies suggest mechanistic links between predation risk and environmental microbiomes.

Predators could also affect soil microbiomes via the spatial distribution of their kills. For example, wolves affect heterogeneity in soil nutrients via the distribution of where they kill moose (Bump et al. 2009). This heterogeneity in nutrient pulses via moose carcasses increases both bacterial and fungal abundance in the soil and changes soil community composition by increasing bacteria relative to fungi. Given that carrion is important to the ecology of many ecosystems (Benbow et al. 2016; see the section below), the link between

predators, soils, and microbes via carrion is likely underappreciated in its importance.

**How do consumer diversity, identity, and body size affect microbiomes?** The diversity of consumers likely affects how intensely the loss of a species cascades through a community (Duffy et al. 2007). As the diversity of consumers increases, the effects of trophic cascades affecting primary producer communities often decline (Bruno and O'Connor 2005, Duffy et al. 2005), suggesting a possible diminution of effects on microbial communities as well. Therefore, systems such as the lakes described above that have low species diversity may exhibit the strongest links between predators and microbes, similar to the links between predators and plants, although this idea remains untested.

Although the diversity of consumers can be important for ecosystem function, examining what happens to microbiomes under realistic scenarios of consumer loss, such as losing the largest consumers first, will be important for estimating the impacts of defaunation on microbe-driven ecosystem processes (e.g., Risch et al. 2018). For example, recent work in African savannas shows that larger herbivores (e.g., elephant, rhino), which are more prone to overexploitation, often have very different effects on plant communities than do smaller herbivores (e.g., impala, warthog; Burkepile et al. 2016, van der Plas et al. 2016). These differential impacts on plant communities likely lead to differences in plant litter accumulation that feeds back to create distinct impacts on soil microbiomes (e.g., figure 2; Cline et al. 2017). In addition, the removal of large herbivores can even affect the microbiome of very small herbivores. For example, the presence of cattle grazing significantly altered the microbiomes of caterpillars, likely via shifts in the plant community and caterpillar diets when the cattle were present (Berman et al. 2018). Therefore, these different-size herbivores likely create very different landscapes of herbivory that differentially affects environmental and host-associated microbiomes that will alter microbe-driven processes and their ecosystem functions.

Along with consumer body size, the origins of consumers may also affect microbial dynamics. Not only are we losing native predators and herbivores in many ecosystems, but we are also replacing these native species with nonnative species that may differ significantly in diet, body size, and behavior (Olden et al. 2004). This reorganization of consumer communities could fundamentally alter the natural impacts of macrobes on microbiomes. For example, nonnative herbivore species often have significantly different effects on plant communities than do native herbivores (Parker et al. 2006), often facilitating invasions of nonnative plant species (i.e., invasional meltdown). These nonnative plants often reshape the physicochemical properties of the soil and, as a consequence, environmental microbiomes (Gibbons et al. 2017). Invasive and nonnative organisms may also provide a more direct route for shifting the microbial ecology of a system by transmitting their own microflora to a permissive



host or ecosystem. Therefore, simply substituting species in the herbivore fauna, without altering the intensity of herbivory, could dramatically reorganize plant communities, soil microbes, host microbiomes, and belowground processes via a variety of pathways.

**What are the bottom-up impacts of defaunation on microbiomes?** The loss of large animals could also directly or indirectly alter bottom-up factors that affect microbial community dynamics and metabolism. For example, the presence of megaherbivores, such as hippopotamuses (*Hippopotamus amphibius*), alter aquatic ecosystem functioning by moving organic matter and nutrients across the landscape. Hippos transfer nutrients from the terrestrial systems where they graze to the rivers where they congregate and rest (Stears et al. 2018). Excessive amounts of feces in hippo pools can result in massive downstream changes in microbial metabolism, including increases in heterotrophy that drive the loss of oxygen in the rivers, causing hypoxic fish kills (Dutton et al. 2018). The exploitation of animals such as hippos, fishes, birds, and ungulates that are important for moving nutrients around the landscape has likely led to dramatic differences in the distribution of nutrients both within and among ecosystems (Doughty et al. 2016). The concomitant impact on the diversity and distribution of the microbes that process those nutrients is poorly understood.

Anadromous Pacific salmon (*Oncorhynchus* spp.) are the classic example of this process, because they vector marine-derived nutrients to aquatic and terrestrial systems during their annual spawning runs from the ocean into streams (Naiman et al. 2002). Because these species typically die after spawning, their carcasses deliver large amounts of marine-derived nutrients to inland ecosystems. These salmon-derived nutrients can alter the diversity of benthic primary producers (Chen et al. 2011), increase the growth of riparian trees (Helfield and Naiman 2001), and alter riparian forest diversity (Hocking and Reynolds 2011).

These animal carcasses also likely have significant impacts on microbiomes and microbial processes (Metcalf et al. 2016, Strickland and Wickings 2016), but the ecological context of these effects is poorly understood because of relatively few studies (Barton et al. 2013, Strickland and Wickings 2016). For example, insects from streams with salmon carcasses had internal microbiomes that were distinctly different from insects from nonsalmon streams (Pechal and Benbow 2016). Importantly, the differences in microbiomes were evident for insect taxa across trophic levels, suggesting that the presence of salmon carcasses and their nutrients altered insect microbiomes across the food web, not just for species that fed on the salmon carcasses. Similarly, whale falls, the deposition of dead whale carcasses, are a classic example of the bottom-up impacts of animal carcasses, serving as important nutrient inputs to the deep ocean (Smith et al. 2015). This huge pulse of nutrients increases benthic animal abundance and diversity and also creates microbiomes in deep-sea sediments unique to whale falls (Goffredi and Orphan 2010). Given the

increasing importance of mass animal mortalities across different ecosystems (Fey et al. 2015), connecting microbiome dynamics to these events would be a productive area of focus.

However, the dearth of research on the bottom-up impact of animals on microbiomes is unfortunate, because populations of large animals are dwindling and carcass-derived nutrients are being significantly reduced by overexploitation (Doughty et al. 2016). For example, salmon currently deliver approximately 400 megatons (MT) of nitrogen and approximately 45 MT of phosphorus to watersheds in the western United States; however, these numbers are at least an order of magnitude below the historical levels of approximately 5000–7000 MT of nitrogen and approximately 600–800 MT of phosphorus before widespread salmon fishing (Gresh et al. 2000). The loss of the amount of nutrients from salmon carcasses and other formerly abundant species likely had a significant influence on environmental microbiomes and their associated processes across large spatial and temporal scales. Similarly, whale populations have declined by 66%–99% over the last century (Doughty et al. 2016), likely resulting in a decline of approximately 80% in the transport of nutrients from the upper ocean to the deep sea via whale falls (Roman et al. 2014). This dramatic decline in the movement of nutrients to the seafloor has likely altered the abundance, diversity, and function of the sediment microbiome across large scales in the deep ocean.

## Conclusions

In retrospect, Wilson and Terborgh were undoubtedly both correct—the big things and the little things both run the world, often in different, complex ways. But these animal consumers also exhibit complex and dynamic feedback loops with the smallest biological entities—bacteria, fungi, viruses, and a cadre of other microscopic organisms. The current mass extinction and climate crises that define the Anthropocene continue to erode our already vanishing biodiversity with increasing evidence showing that these losses affect microbiomes in a variety of ways. Currently, these feedback loops among macrobes and microbes are likely underappreciated. Research that can continue to reveal the extent and strength of these interactions from the top most predators, through herbivores, to foundation species and their microbiomes is increasingly needed. We encourage ecologists and microbiologists to continue to embrace fruitful new avenues of research that focus on feedback loops between macrobe- and microbe-mediated processes. Such effort will help us understand how long the arm of defaunation truly is and how it affects all levels of biological organization.

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