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Special Focus: Microbes in Biogeochemical Cycles during Climate Change
Review

Trophic Regulations of the Soil Microbiome

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The soil microbiome regulates vital ecosystem functions ranging from primary production to soil carbon sequestration. Yet, we have only begun to understand the factors regulating the soil microbiome. While the importance of abiotic factors is increasingly recognized, the roles of trophic regulations in driving the structure and function of the soil microbiome remain less explored. Here, we review the current understanding of how and when microbial and top predators of the soil shape the community structure and function of the soil microbiome via both direct and indirect effects. We finally highlight that the structure and function of the soil microbiome depend on the interactive effects among predation, plant inputs, and abiotic variables present in the soil.

The Main Regulators of the Soil Microbiome

Most of the living biomass on Earth is comprised of microorganisms [1]. Soil, in particular, harbours an enormous diversity and abundance of microbial life referred to, collectively, as the soil microbiome [2,3]. The soil microbiome is mainly comprised of soil bacteria and fungi, which reside in the **bulk** and/or in the **rhizosphere soil**. The diversity and abundance of soil bacteria and fungi are responsible for a vast number of vital ecosystem functions and services, such as primary production, carbon sequestration, and nutrient mineralization [4]. Ecologists and microbiologists have thus sought for a long time to understand the factors that regulate the structure, composition, and function of soil bacteria and fungi.

It has been suggested that soil abiotic properties, such as pH and organic matter content, are the principal regulators of the structure and composition of soil bacteria and fungi [2,5]. Moreover, studies have consistently shown that the community composition of soil bacteria and fungi also depends on several biotic factors [6,7]. Broadly, there are two biotic factors that regulate soil bacterial and fungal communities, particularly at the finer spatial scales: litter input and **rhizodeposition** by plants, and **top-down regulation** by the predators of bacteria and fungi. While the important role of plant inputs **(bottom-up regulation)** in influencing the soil microbiome at various spatial scales has received greater attention [8,9], the role of a wide range of soil predators that directly and indirectly affect soil bacterial and fungal communities has received relatively less attention in the soil microbiome literature [2,10].

Community ecologists have consistently shown that predation is one of the major biotic forces responsible for structuring ecological communities [11,12]. As we will argue, the soil microbiome is no exception. In general, the net effects of predation on prey communities operate via two mechanisms: first, by direct consumptive effects on prey population, and second by indirect effects on **basal resources**, which are driven mainly via the changes in prey density and prey traits [13,14]. Our aim in this review is to outline the direct and indirect pathways by which microbiome predators regulate the structure and function of the soil bacteria and fungi. We aim to highlight that microbiome predators regulate the structure and function of the soil microbiome via both preferential and nonpreferential feeding, influencing the competition within and between soil bacterial and fungal communities. We further elaborate on how such trophic regulation of the soil microbiome can interact with plant resources and abiotic factors, helping to scale-up the

Highlights

Predators of the soil microbiome regulate microbial structure and functions via both preferential and nonpreferential feeding, with implications on their structure (e.g., diversity) and functions (e.g., nutrient mineralization).

The trophic cascade effects on the soil microbiome is often masked due to intraguild predation and omnivory in the soil.

Less is known about how microbiome predators influence the competition between soil bacteria and soil fungi.

Global climate change can alter the trophic ecology of the soil microbiome by making it fungus-dominated, depending on soil moisture and resource availability.

We propose that the interaction among microbiome predators, plant inputs, and abiotic resources could interactively determine the structure of the soil microbiome.

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importance of microbiome predators at the larger spatial scales. We finally discuss how climate warming and drought can alter the trophic ecology of the soil microbiome.

Key Predatory Groups and Their Direct Effects on the Soil Microbiome

In this review, we refer to soil fungi and soil bacteria collectively as the soil microbiome. The other components of the soil microbiome, such as protists and viruses, are treated as the consumers within the soil microbiome (Box 1). Broadly, there are four groups that consume the soil microbiome (Figure 1): (i) protists (within the soil microbiome) (Box 1); (ii) free-living soil nematodes; (iii) soil microarthropods; and (iv) **saprophagous soil animals** [15,16]. Among the four groups, protists, nematodes, and microarthropods are the direct predators of the soil microbiome, whereas saprophagous soil animals, such as earthworms and isopods, ingest bacteria and fungi via feeding on soil and soil organic matter. Importantly, these organisms that feed on microbes represent a large gradient in their body size, ranging from a few millimeters to a few centimeters [17,18]. Moreover, as the body size varies among the consumers of soil microorganisms, their net consumption also varies; this imposes differential effects on the soil microbiome [19].

Free-living soil nematodes are one of the major consumers of the soil microbiome with groups that feed on bacteria and fungi [31,32]. Bacterial-feeding nematodes – representing half of all soil nematodes – are **generalists** that randomly ingest any bacteria by their filter-feeding habit [33,34]. Fungal-feeding nematodes, by contrast, penetrate fungal hyphae by their stylet or spear [33]; they have been shown to limit hyphal growth in soils [33,35]. Soil microarthropods, particularly Collembola and mites, are the other key direct consumers of the soil microbiome. Al-

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Box 1. Predation within the Soil Microbiome

The soil microbiome consists not only of the commonly studied bacteria and fungi, but also a major group of microbiome predators – protists. Protists feed mainly on soil bacteria [16], reducing both abundance and changing the community composition of bacteria through specific prey selection [20]. Generally, protists avoid too large or toxin-producing bacteria, such as pseudomonads, as well as increase the ratio of Gram-positive to Gram-negative bacteria through preferential feeding on easier-to-digest Gram-negative bacteria [20,21]. These taxonomic changes in microbial communities have been found to result in functional changes that can result in enhanced plant performance [21]. A majority of protists also feed on fungi [22], whereas larger protists are often **omnivores**, feeding simultaneously on different microbial groups, such as bacteria, fungi, and smaller protists [21].

Viruses are another important regulator of the soil microbiome. Despite the arguments whether viruses are truly a living form, viruses are often considered as part of the microbiome [2]. Viruses, as key agents (bacteriophages) of bacterial mortality, have been widely studied in aquatic systems, and their presence in high abundance with high diversities has been confirmed for soils [23,24]. Considering that many bacteriophages are often highly host-specific, viruses likely change the composition of bacterial communities. Viruses infecting fungi (mycoviruses) can further alter the structure of fungal communities [25].

Diverse groups of bacteria and fungi also kill other microorganisms through the production of antimicrobial compounds in the soil. This often results in increased growth rates of the antimicrobial compound-producing microorganisms as competitors for limiting nutrients are eliminated, while also additional nutrients from the killed competitors become available [26]. Indeed, some bacterial groups, such as myxobacteria, have developed to obtain their nutrients through lysis of other bacteria [27], while other bacterial groups, such *Collimomas* spp., have specialized to use fungi as their main nutrient source [28].

While our focus in this review is on the soil microbiome predators, we need to highlight the importance of parasites in indirectly structuring soil microbiomes by parasitizing predators of microorganisms. Among them are viruses, bacteria, fungi, and protists. So far, we have only begun to understand the diversity of some of these parasites in soils and soil animals [29,30]. The role of these animal parasites in shaping animal communities in soils, and their effect on the soil microbiome, remains to be elucidated.

Glossary

Apparent competition: an indirect form of competition between or among prey species when they share a common predator, but with preferential feeding on one over the other prey.

Basal resources: resources (living or nonliving) that form the base of food-web pyramids.

Bottom-up regulation: the regulation of predators or consumers by their prey or resources.

Bulk soil: the soil not influenced by plant roots.

Density-mediated indirect effects: effects that occur when changes in the abundance (or the biomass) of predators affect the density (or the biomass) of prey through direct predation, which, in turn, changes densities (or the biomass) of resources of prey.

Generalists: those predators feeding on several prey species.

Intraguild predation: the process of one predator feeding on another predator.

Keystone predator: predator species that can strongly affect the structure of prey communities without being higher in density.

Omnivores: consumers that can feed on multiple trophic levels.

Rhizodeposition: the release of chemical compounds by plant roots into the rhizosphere soil.

Rhizosphere soil: the soil immediately adjacent to plant roots.

Saprophagous soil animals: soil animals which feed on dead organic matter.

Top-down regulation: the regulation of prey or resources by their predators or consumers.

Top predators: predators belonging to the top of the food chain, which, in this study, refers to those feeding on direct predators of the bacteria and fungi as well as saprophagous animals.

Trait-mediated indirect effects: effects that occur when changes in the abundance (or the biomass) of predators affect the trait (e.g., morphological, physiological, or behavioural) of prey through direct predation, which, in turn, changes densities (or the biomass) of the resources of prey.

Trophic cascades: indirect species interactions originating with top predators and spreading downwards through food webs.
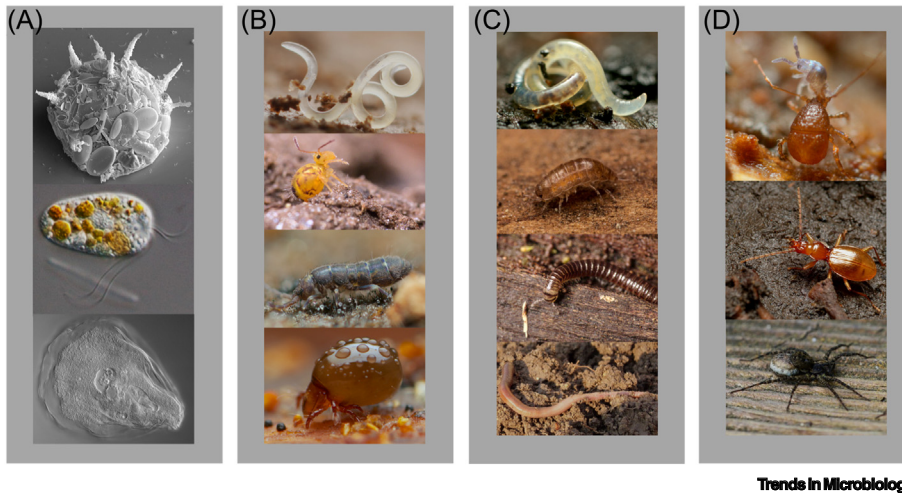
Figure 1. Four Major Groups of Consumers in the Soil That Directly and Indirectly Affect the Soil Microbiome. (A) Within-microbiome predators (mainly protists, Box 1). (B) Direct predators of the soil microbiome (mainly nematodes and microarthropods). (C) Saprophagous soil animals that feed on the soil microbiome via their feeding on dead organic matter (enchytraeids, isopods, millipedes, and earthworms). (D) Top predators of the soil (predatory mites, beetles, and spiders) that feed mainly on direct predators and saprophagous soil animals. Images reprinted with permission from Andy Murray, Eckhard Voelckler, Steffen Clauß, Sarah Zieger, https://pixabay.com.

though collembolan species feed on soil bacteria [36,37] and plant materials [38], the majority of Collembola species feed mainly on soil fungi [39,40]. Among soil mites, oribatid mites are the major group that feed on a wide range of fungal species, such as on dark-pigmented fungal groups and ectomycorrhizal fungi in forest ecosystems [36,41]. Some of the major consumers of soil microorganisms are in fact the ones that do not predate on them but rather consume them via the consumption of soil, litter, and soil organic matter, such as earthworms, isopods, millipedes, and enchytraeids. Among them, earthworms are the most dominant consumer (in terms of amount consumed) of the soil microbiome in most systems [42,43]. The earthworm's ingestion rate and assimilation efficiency of organic matter are the key determinants of how they influence the structure and function of the soil microbiome [42]. In general, higher assimilation efficiency in some of the earthworms, such as those dwelling on the soil surface, promotes microbial growth in the soil [44]. However, those earthworms with greater assimilation efficiency usually have the lower ingestion rates of organic matter [42]. These differences among earthworms relate to their selective versus predominantly nonselective feeding on soil organic matter. An earthworm's gut passage can also act as an environmental filter for certain soil microorganisms, for example, by suppressing the colonies of bacteria and inhibiting the germination of spores and radial growth of fungal species [45,46].

Most soil microbiome predators exhibit preferential feeding on some prey over others. For instance, both bacterial- and fungal-feeding nematodes exhibit preference for some prey based on prey traits and the soil environment [35,47]. Further, fungal palatability might determine the diet preference by collembolan species [48]. Oribatid mites often prefer dark-pigmented fungi, which are crucial biotic drivers of litter decomposition [41]. The preferential feeding in earthworms, based on the quality of the litter, has also been reported by several studies [42,49]. Importantly, the vast physical structure present in the soil [50] can constrain or facilitate preferential feeding on the soil microbiome. Such predominant preferential feeding among the microbiome predators can have important implications for the soil microbiome structure and function, such as competitive interactions between soil bacteria and fungi (see Figure I in Box 2).

Box 2. Predator-Mediated Competition between Soil Bacteria and Fungi

Soil microbial ecology has long investigated the competitive interactions between bacteria and fungi. The general notion is that they compete for simple plant-derived substrates with important implications on microbe-mediated processes in the soil [26]. A recent study also revealed that bacterial and fungal competition is strongly present in the top soil across the globe and is mediated by antibiotic-resistance genes [7]. Negative interactions between fungi and soil bacteria can reduce the turnover of soil organic matter [72]. Microbiome predators can further influence the competition between soil bacteria and fungi in numerous ways. For instance, fungi can have greater competitive advantage over bacteria when bacterial predators become dominant or more active (the same applies to competitive advantage to bacteria when fungal predators are dominant). However, these pathways of bacterial and fungal trophic regulation by their predators can also be highly connected; that is, many bacterial predators do not exclusively forage on bacteria but only preferentially do so (the same holds for fungal predators) (Figure I). Shared predators thus can also lead to **apparent competition** between soil bacteria and fungi. Furthermore, we stress that differential feeding rates on distinct bacteria or fungi can lead to major changes in bacteria to fungal dominance that need to be adequately addressed when predicting the soil microbiome (Figure I). Saprophagous consumers and top predators can also indirectly influence the competitive interaction between fungal and bacterial groups, such as via altering their habitat and trophic cascades, respectively. Besides, these predator-mediated competitive interactions in the soil microbiome can also occur within microbial groups, such as within fungi and within bacterial groups. Empirical evidence for predator-induced competitive interaction between soil fungi and bacteria is still scarce. Moreover, as shown by both theoretical and empirical studies, the interaction between predation and competition is one of the key determinants of variations in community structures [73,74] and has rarely been tested in understanding the soil microbiome community structures. We believe that experimental approaches can help us to understand the importance of predator-induced competitive interaction between and within the bacterial and fungal groups.
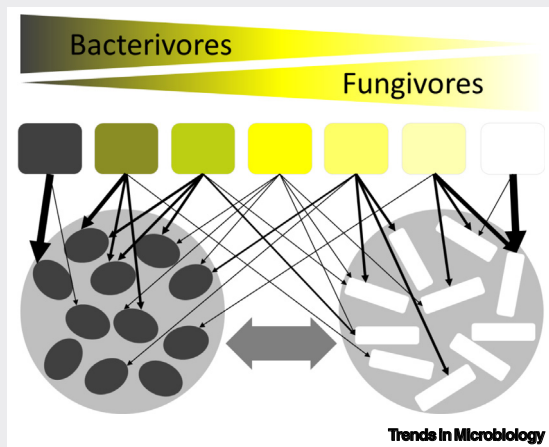

Figure I. Degree of Preferential Feeding between the Two Categories of Microbiome Predators. Bacterivores are bacterial predators while fungivores are fungal predators. These predators affect the interaction (e.g., competition) within and between fungal and bacterial communities.

All microbial-feeding groups influence microbe-mediated ecosystem processes in the soil by affecting microbial population and traits. These processes range from increasing nutrient turnover to increasing decomposition rates to influencing plant performance [15]. For instance, bacteria-feeding predator groups have been shown to enhance the turnover rates of soil bacterial communities, particularly in the environment where resources for soil bacterial communities are sufficient, such as greater amounts of organic matter potentially in proximity to plant roots [51,52]. In such cases, predators of bacteria increase the rate of nutrient mineralization and the decomposition of organic matter in the soil [53], thereby benefitting plants [54]. Fungus-feeding predator groups also affect plant performance and the decomposition process in a number of ways by feeding on soil fungi. For instance, they negatively affect the performance of mycorrhizal host plants when they feed on mycorrhizal fungi [55,56], but also could enhance the nutrient mineralization process via their stimulation of decomposer fungal communities with potential benefits to plants [57].

Indirect Effects of Top Predators on the Soil Microbiome

Direct predators of the soil microbiome are further consumed by other carnivores in the soil, and they thereby exert indirect effects on the soil microbiome. Such indirect effects of predators of the soil microbiome predators (hereafter **top predator** for brevity) on the soil microbiome operate via two interdependent mechanisms (Figure 2): **density- or biomass-mediated indirect effects** and **trait-mediated indirect effects** [58]. Density-mediated indirect effects are often studied as **trophic cascades** [14]. Theoretically, the greater the prey suppression by the predator the larger is the strength of trophic cascades. Trophic cascades on the soil microbiome have mainly been demonstrated via predator-removal experiments [15]. For instance, Santos *et al.* [59] experimentally showed that the removal of predatory mites which feed on microarthropods and nematodes suppressed bacterial population size, which, in turn, reduced decomposition rates in a desert soil. In another removal experiment, but with spiders, which are larger predatory species of microarthropods, a similar cascading effect was observed on litter decomposition, but only in drier conditions [60].

The three key groups of microbial consumers discussed above (nematodes, microarthropods, and saprophagous animals) have their own group of predators (Figure 1), and it is thus likely that these **top predators** exert distinct cascading effects on the soil microbiome [19,61]. In fact, some of these top predators are large enough to prey upon the predators of other groups, which typically results into **intraguild predation** [62]. Intraguild predation can potentially dampen the strength of trophic cascades in food webs [61]. Owing to a greater probability of intraguild predation among the predators of microbe-feeding species, the size and structure of the soil microbiome are lesser affected by top predators [63]. The same has been argued for widely present **omnivory** in the soil [64], which potentially reduces the prevalence of **keystone predators** in structuring prey communities [65,66] as observed in other systems [67]. In fact, several top predators in their juvenile stage feed on soil fungi and bacteria but change their diet to direct predators
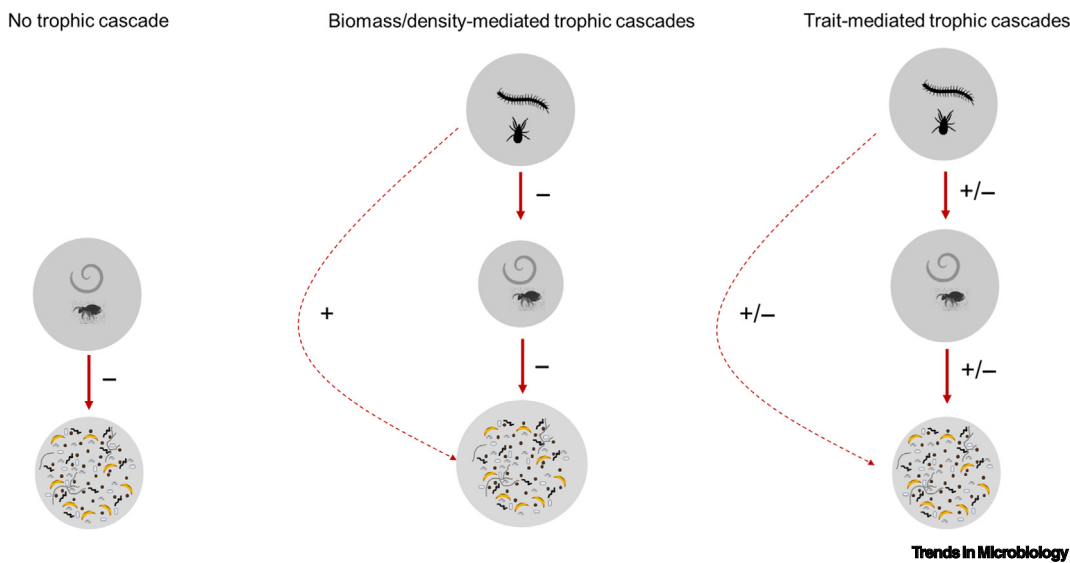

Trends in Microbiology

Figure 2. Illustration of Density- and Trait-mediated Trophic Cascade Effects on the Soil Microbiome. Trophic cascades occur only in the presence of top predators (at least three trophic levels). In density-mediated trophic cascades, top predators increase the density/biomass of the soil microbiome (indicated by the larger grey circle) by reducing the density/biomass of microbiome predators (smaller grey circle). In trait-mediated trophic cascades, the effects of top predators on the soil microbiome can be both positive or negative depending on which predator traits are affected. The density/biomass of microbiome predators may not change in trait-mediated effects (shown by larger sized grey circles for microbiome predators compared with density-mediated trophic cascades). The broken lines indicate the indirect effects.

of the soil microbiome as they develop into adults. However, the effects of removal of top predators can manifest in soil processes carried out by the soil microbiome, such as decomposition and nutrient mineralization, even without a noticeable change in microbial community size [68].

Trait-mediated indirect effects in food webs often depend on how top predators influence the behaviour of their prey without affecting their population size (Figure 2), which then influences both the population and traits of the resources of the prey. When applying this to the soil microbiome, top predators should cause behavioural shifts (and potentially other trait changes, such as morphological and physiological changes) in microbial consumers to the extent that noticeable change occurs in microbial population, trait, and/or function. However, the role of trait-mediated indirect effects on the soil microbiome is far less understood as the traits of microbiome predators have often been ignored in soil food-web studies [69]. Evidence of behavioural shifts in the consumers of soil microorganisms owing to top predators has shown that soil microbial-mediated processes, such as soil respiration and N_2O emissions, can substantially change [70, 71]. It is thus likely that the structure of the soil microbiome is prone to change via the nonconsumptive effect of top predators on microbial consumers, and this merits further exploration.

Relative Importance of Abiotic and Predator-Mediated Impacts on the Soil Microbiome

We have yet to reach a quantitative understanding of the drivers that govern the structure and function of the soil microbiome. The current assumption is that the soil microbiome is almost completely structured by abiotic factors, such as pH and moisture, particularly at larger spatial scales [2,75]. Yet, there is profound evidence that biotic effects also play a role in structuring the soil microbiome (Figure 3). This is most evident from studies that show bottom-up effects of how plants shape their associated microbiome, such as bacteria [76] and mycorrhizal fungi [77]. More recently, interactions within the soil microbiome have been placed as a central component in regulating the soil microbiome structure. In particular, the competition for nutrients determines interactions between bacteria and fungi [7] (Box 2).

In contrast to abiotic processes, bottom-up and competition-driven factors, and the relative role of predators in shaping soil microbiomes, remain nearly unknown. At finer spatial scales (e.g., close to rhizosphere soil or related to the body size of the predator in the study), predators
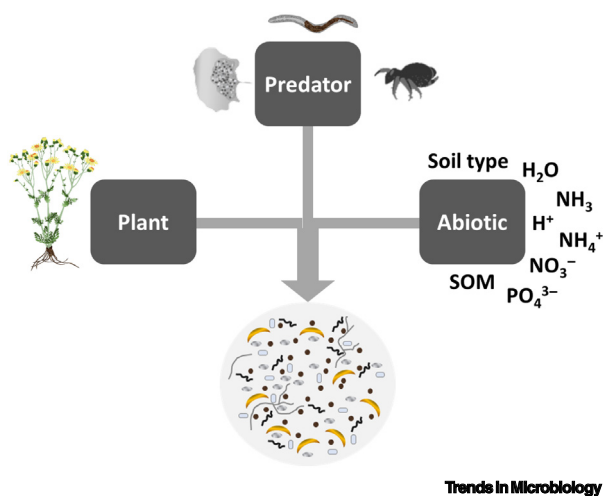

Trends in Microbiology

Figure 3. Interactive Effects among Microbiome Predators, Plant Inputs and Abiotic Factors Can Influence the Structure of the Soil Microbiome. Please note that the soil microbiome can also feed back to all three components.

have been shown to control both the abundance and the composition of the microbiome, as is most evident for bacteria and their predators [54]. Microbiome predators can also shift the composition between bacteria and fungi, such as by increasing the bacteria/fungi ratio when there is a dominance of predators that preferentially feed on fungi [78] (Box 2). These few specific examples have yet to be compared with the abovementioned abiotic-, plant-, and competition-driven changes in order to disentangle the relative importance of predation in structuring soil microbiomes (Figure 3). For that, integrative experimental studies that simultaneously manipulate abiotic parameters, plant species, and predators are needed. Furthermore, such an approach is important given that climate change continues to alter all of these factors together with the soil microbiome [79] (Box 3). Global surveys targeting microbiomes need to be supplemented with information on microbiome predators, which could provide newer insights on the key drivers of changes in the soil microbiome.

Outlook: Scaling-Up of Trophic Regulation from Local to Global Scales

Knowledge of the trophic ecology of soil microorganisms is expanding on numerous fronts. For instance, recent advances in tracing nutrient flows from microorganisms to their predators, using stable isotope techniques and molecular gut-content analyses, have shed new insight on the feeding niches of several microbiome predators [91]. Trophic cascade and trait-mediated studies have further pointed out the importance of top predators in the soil that could influence some of the key soil microbiome functions [92,93]. While we consider that the structure and function of the soil microbiome at the finer spatial scales can only be better predicted by an adequate consideration of their predators, we have ignored the importance of predators in influencing the soil microbiome structure and function at larger spatial scales (e.g., [2]).

Recent global analyses of the soil microbiome have duly noted the importance of biotic interactions, such as competition between soil bacteria and soil fungi [7]. As we argued that microbiome

Box 3. Climate Change Effects on Trophic Regulation of the Soil Microbiome

A global rise in the Earth's surface temperature and more erratic rainfall patterns posit key threats to biodiversity [80]. Both soil microorganisms and their predators are vulnerable to such changes in soil temperatures and soil water availability [81], although the vulnerability may vary among the study groups [82,83]. Importantly, the rate of predation by ectothermic organisms (all soil microbiome predators discussed in this review are ectotherms) often becomes higher at warmer temperatures due to elevated metabolic demands. However, this is only true until a certain temperature threshold beyond which predators die due to physiological constraints at high temperatures [84]. The basic notion of metabolic ecology is that ectotherms with larger body sizes have lower temperature thresholds than smaller ones [85], which accordingly makes larger microbiome predators more sensitive to warming. In an experimental study, increase in temperature altered the physiology of microbiome predators by reducing their body size, which only occurred in a microbiome predator with a larger body size [86]. Thus, while temperature enhances the foraging demand of microbiome predators, it also triggers phenotypic responses in microbiome predators that could balance their foraging demand.

The implications of greater foraging pressure by predators and their physiological adaptations can vary in time, and thus each of these stages (the adaptation process) may have distinct impacts on their microbial prey. This will further interact with how microorganisms themselves respond to increases in temperature, including their physiological adaptation. Soil fungal and bacterial responses to warming are often dependent on soil water and resource availability [79]. For instance, drier and warmer soil seems to harm bacteria more than fungi, although this may again differ among the soil types [87,88]. If both fungal and bacterial predators become active proportionally at higher temperature, it is likely that warming could favour fungal communities in the soil. Drier soil conditions, in particular, can lower the foraging efficiency of several soil microbiome predators in warmer soils [89]. The implications of reduced foraging of soil microorganisms can slow down the stimulation of their population which often takes place via their consumption, such as for soil bacterial communities [51]. Although soil bacterial communities can overcome such a competitive inferiority via their physiological adaptation to higher temperatures, a recent meta-analysis showed that the physiological adaptation of soil bacteria and fungi did not systematically vary over time in warming experiments [90]. We therefore encourage future global-change studies to consider both the physiological adjustments in microorganisms and their predators to capture a better understanding of their dynamics in a changing world.

predators can influence the competition between soil bacteria and soil fungi in several ways, it is likely that information on microbiome predators can shed light on the global variability in soil microbiome patterns. A recent global study on latitudinal patterns of predation strength on insect prey showed that predation was stronger at lower latitudes than at higher ones [94]. Greater predation could result in higher diversification rates as well as promotion of coexistence of prey species via greater apparent competition. As soil microbial diversity was also recently shown to peak at the lower latitudes [95], we consider that part of it could be related to the variation in predation pressure by microbiome predators across latitudes. Future global-scale studies can shed greater insight on whether the global patterns of predators of the soil microbiome match with the global patterns of soil microorganisms (see Outstanding Questions). Moreover, we advocate simultaneous study of the soil microbiome and its predators, while also investigating soil abiotic properties and vegetation for making microbiome research more predictive (Figure 3).

Concluding Remarks

The importance of top-down control in regulating communities has long been argued in community ecology, which is gaining recognition also in macroscale ecology for predicting community patterns. We believe that increasing interest in understanding the soil microbiome structure and functions at both the microscale and macroscale should adequately consider the importance of the predators. We have argued that microbiome predators interact with other factors such as soil abiotic properties and plant-derived resources in influencing the soil microbiome. However, the overwhelming evidence of preferential feeding, intraguild predation, and omnivory obscures predicting the soil microbiome via trophic approaches. We thus advocate for experimental approaches that can simultaneously integrate predation and abiotic factors in understanding the soil microbiome structure and function at multiple scales.

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