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Microbiome predators in changing soils

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Abstract

Microbiome predators shape the soil microbiome and thereby soil functions. However, this knowledge has been obtained from small-scale observations in fundamental rather than applied settings and has focused on a few species under ambient conditions. Therefore, there are several unaddressed questions on soil microbiome predators: (1) What is the role of microbiome predators in soil functioning? (2) How does global change affect microbiome predators and their functions? (3) How can microbiome predators be applied in agriculture? We show that there is sufficient evidence for the vital role of microbiome predators in soils and stress that global changes impact their functions, something that urgently needs to be addressed to better understand soil functioning as a whole. We are convinced that there is a potential for the application of microbiome predators in agricultural settings, as they may help to sustainably increase plant growth. Therefore, we plea for more applied research on microbiome predators.

INTRODUCTION

Microbiome predators are increasingly studied in soils as more evidence points to their roles in shaping the soil microbiome (Geisen et al., 2018). Through microbiome modifications, microbiome predators have a major impact on soil functioning, such as catalysing litter decomposition (Geisen et al., 2021) and enhancing plant performance (Gao et al., 2019; Guo et al., 2022). Microbiome predators include all organisms that feed on members of the microbiome (viruses, bacteria, archaea, fungi) (Geisen et al., 2018; Thakur & Geisen, 2019). The most abundant and important groups of microbiome predators are protists and nematodes as the major consumers of bacteria (Bar-On et al., 2018; de Ruiter et al., 1995). Protists and nematodes also feed on fungi but have a weaker role in this energy channel than Collembola and mites (de Ruiter et al., 1995). Here, however, we focus on protists and nematodes, as they are the most abundant microbiome predators that affect both bacterial and fungal communities.

Microbiome predators prey on diverse soil organisms (Geisen et al., 2020). As predators of bacteria or fungi, they are key members of bacterial or fungal energy channels (de Ruiter et al., 1995; Hunt et al., 1987). Many microbiome predator species are generalists like other soil organisms and feed omnivorously on many bacterial and fungal species in both channels (Anderson, 1975;

Digel et al., 2014; Geisen, 2016; Potapov et al., 2022). Viruses are also preyed on by protists and nematodes, representing a link beyond classical energy channels (Deng et al., 2014). Even more, intraguild predation among microbiome predators seems to be common; already classical food webs propose that small flagellated protists are major prey of larger amoebae and nematodes (de Ruiter et al., 1995). More recently, inverted food webs were shown with smaller protists (and other small biotas, such as myxobacteria (Petters et al., 2021), not covered here) preying on larger organisms, including nematodes (Geisen et al., 2015). This complexity of diverse predator–prey links hampers a reliable placement of distinct microbiome predator species in soil food webs and, consequently, the understanding of their precise functions in soils.

Fundamental studies on the functioning of microbiome predators currently are focused on a few microbiome predator species (Geisen et al., 2017), while field studies mostly investigate patterns of microbiome predator communities without testing their role in soil functioning. These approaches conflict with the fact that potentially millions of functionally diverse microbiome predator species exist (Geisen, Wall, & van der Putten, 2019). We now know that microbiome predators have species-specific feeding differences that can change microbiome composition and functioning (Amacker et al., 2022; Glucksman et al., 2010), which can explain the major impact of microbiome predators on the microbiome (Geisen et al., 2016; Saleem et al., 2012). Yet, we are missing an understanding of the functional importance of microbiome predator communities for key ecosystem functions that soils provide, such as elemental cycling and plant performance (including growth, health, and yield).

Even less is known about microbiome predators functioning in soils exposed to ongoing global changes, including those in climate and land use. Several studies are showing that abiotic conditions are major determinants of protist and nematode communities, particularly soil moisture, structure, pH, and carbon availability (Dupont et al., 2016; Erktan et al., 2020; Oliverio et al., 2020; van den Hoogen et al., 2019). All these factors are subject to change as drought, warming, and other climate change events are anthropogenically catalysed (Dai, 2013), while the need for land to meet human needs is rapidly rising (Seto et al., 2012). These global change drivers (GCDs) all affect biodiversity and soil functions, but how they affect microbiome predators and their impact on microbiome functioning remains unknown.

The extensive number of fundamental knowledge gaps also hampers the evaluation of the functional role of microbiome predators in agricultural systems. Protists and nematodes have long been claimed to serve as sensitive indicators of soil health (Du Preez et al., 2022; Foissner, 1997) and were repetitively shown to improve crop health and production (Guo et al., 2022; Zheng et al., 2022). As such, there is clear evidence of the potential of microbiome predators for application, but this remains a largely untouched field. To provide the basis for some next steps in increasing our understanding of microbiome predators in soil, we here pose three major questions that should be focused on in future research:

1. What is the importance of microbiome predators in soil functioning?
2. How do global changes impact microbiome predators?
3. Are microbiome predators applicable such as in agriculture and if so, how?

While the first two are the basis to better understand the functioning of soil microbiome predators in current and future soils, we see the third as the needed link between fundamental science and potential application.

WHAT IS THE ROLE OF MICROBIOME PREDATORS IN SOIL FUNCTIONING?

The positive roles of microbiome predators in ecosystem functioning are particularly linked to plant performance, for example, growth, health, and yield. Through predation, microbiome predators release the nutrients inside their prey (nitrogen, phosphorus, or silica) or enhance prey activity to mobilize these nutrients (Jiang et al., 2023; Puppe, 2020; Ranoarisoa et al., 2020), which then become available and increase plant growth (Figure 1; Thakur & Geisen, 2019). Microbiome predators might also promote pathogen-suppressive microorganisms via changes in the community composition (Gao et al., 2019; Guo et al., 2022; Thakur & Geisen, 2019) and feed on plant pests and pathogens, thereby reducing plant diseases (Figure 1; Geisen et al., 2016; Schwelm et al., 2023). Additionally, microbiome predators play a role in carbon cycling, by enhancing litter decomposition (Figure 1). For instance, the addition of a single protist species increased CO_2 release and catalysed litter decomposition by 35%, through changing microbiome composition and increasing bacterial and fungal activities (Geisen et al., 2021). Theoretically, and not reported yet, microbiome predators could also have negative effects on plant performance by preying on plant growth-promoting organisms, such as arbuscular mycorrhizal fungi, which contribute to litter decomposition and protect their host plants against pathogen infection (Gui et al., 2017). Knowledge of those ecosystem functions driven by microbiome predators is limited and often based on a few microbiome predator taxa, plant species, and ecosystem functions (Mawarda et al., 2022; Saleem et al., 2012). We thus still lack a global understanding

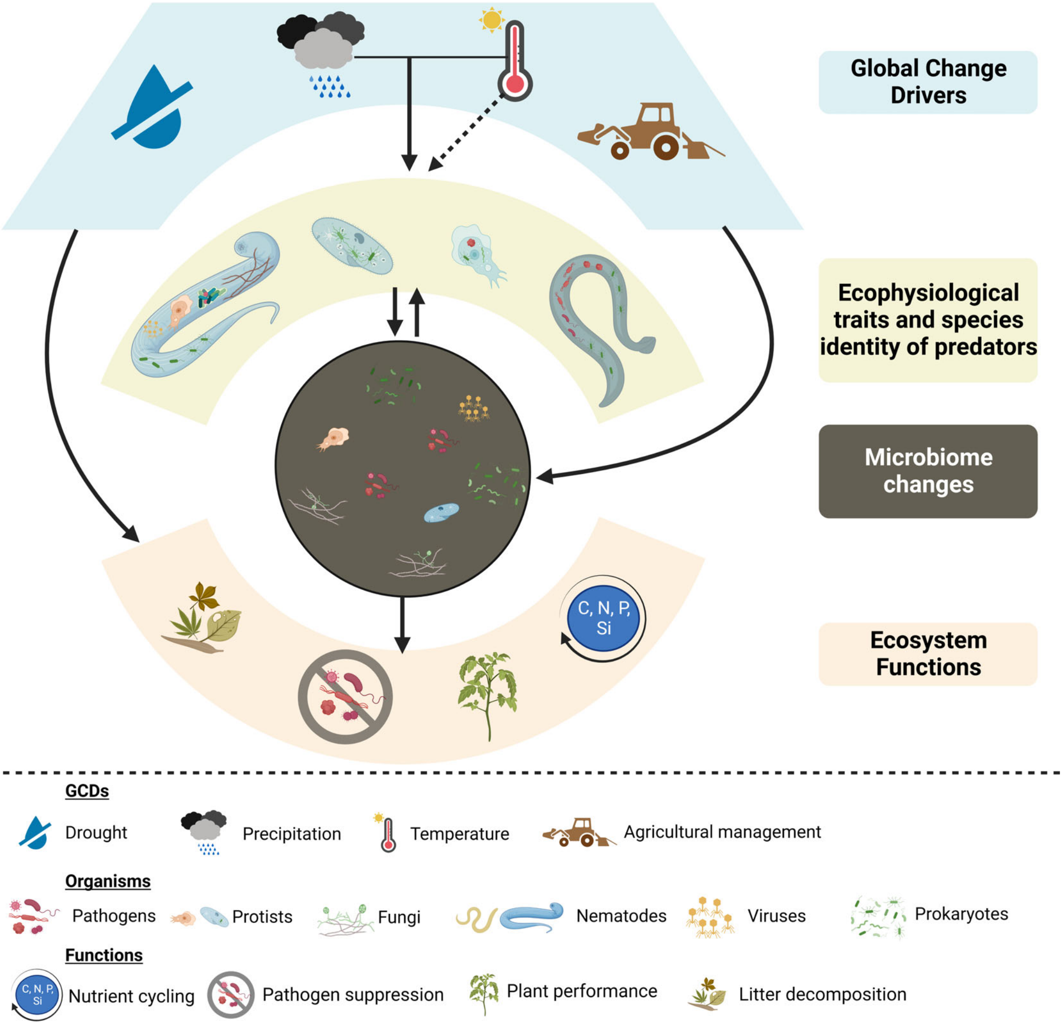

FIGURE 1 Conceptual representation of the intimate link between soil microbiome predators and the microbiome leading to changes in ecosystem functions. Individual (dashed line, here using temperature as an example) or interactive (perpendicular lines, here connecting precipitation and temperature as an example) global change drivers affect these links. Arrows indicate a direct impact on microbiome predators, microbiome, or ecosystem functions. Symbols are explained at the bottom after the horizontal dashed line. Plant performance includes for example, growth, health, and yield.

of how microbiome predators affect plant performance, such as growth, health, and yield, and even more so on other ecosystem functions, such as the cycling of carbon, phosphorus, or silica.

The focus on a few model taxa used to determine the functional role of microbiome predators is in stark contrast with the enormous diversity of microbiome predators present in soil systems (Geisen, Briones, et al., 2019), showing vast morphological, genetic, and, consequently, trait differences (Adl et al., 2012; Bardgett & van der Putten, 2014; Burki et al., 2021). This ecophysiological diversity (here understood as functional traits that determine ecological niches; Gravel et al., 2016) is consequently linked to differential microbiome predator impacts on microbiome composition and its functions, such as carbon or nitrogen cycling (Figure 1). Traits of protists that shape microbiome composition can be species specific (Amacker et al., 2022), and include differences in body size, growth rate, and motility (Dumack et al., 2020; Gao et al., 2019; Olive et al., 2022). For nematodes, body size (length and width) and feeding structures are key traits determining feeding preferences and impacts on microbial communities (Bongers & Bongers, 1998; Semprucci et al., 2018). Despite existing insights on the correlation between microbiome predator traits and their influence on microbiome composition and functioning, the linkage between ecophysiological traits of microbiome predators and soil functioning remains uncertain. Additionally, it is unclear whether community-level traits can serve as predictive indicators for changes in ecosystem functions resulting from alterations in microbiome predator communities (Figure 1).

The relationships between the taxonomic or ecophysiological trait diversity of microbiome predators and their impacts on soil functioning are not yet known.

Following the biodiversity-ecosystem functioning (BEF) concept described, for example, aboveground plant communities, in which increasing plant diversity often positively and linearly relates to ecosystem functioning (e.g., increased plant biomass; Cardinale et al., 2012), we could expect a similar pattern for the relationship between microbiome predator diversity and soil functioning. However, there are major differences between aboveground and belowground diversity, suggesting that soil BEF (sBEF) relationships might be different from the ones described aboveground (Berlinches de Gea et al., 2023; Saleem et al., 2019). For instance, microbial predators are in several ways more diverse than plants (e.g., phylogenetically), but many species may still have similar ecological roles in the ecosystem (Geisen, Wall, & van der Putten, 2019), quickly resulting in functional similarity (Eisenhauer et al., 2023; Saleem et al., 2019). Keystone taxa, which are defined as species having a disproportionally influential role for a given function (Banerjee et al., 2018), might also exist among microbiome predators (Guo et al., 2021). These taxa could exert major predatory pressure on the microbiome compared with other microbiome predator taxa, which might be determined by their ecophysiological traits and prey specialization (Duffy et al., 2007). The varying degree in strength and impact of predator organisms on the microbiome might change the sBEF relationship into more variable rather than linear patterns (Saleem et al., 2019). As keystone taxa among microbiome predators are hardly known, information regarding how differences in diversity and taxonomic compositions of microbiome predator communities affect ecosystem functions is still lacking.

In summary, a framework linking the vast diversity of microbiome predator species and their functional traits to their impacts on soil functioning is currently missing. This leads us to the following questions for future research:

1. What are the main ecosystem functions performed by microbiome predators?
2. Can the impacts of microbiome predators on the microbiome, and therefore on ecosystem functioning, be predicted by their ecophysiological traits?
3. Is the magnitude of ecosystem functioning determined by microbiome predator diversity and what is the contribution of microbiome predator keystone taxa in sBEF relationships?

HOW DO GLOBAL CHANGES IMPACT MICROBIOME PREDATORS?

Anthropogenic GCDs can strongly, and often negatively, affect the community composition, abundance, and diversity of microbiome predators (Thakur & Geisen, 2019; Wilschut & Geisen, 2021). These GCDs include climate change-related factors (e.g., rising soil temperatures, droughts; Hu et al., 2022; Mueller et al., 2016; Thakur et al., 2019), land use change (e.g., fertilization and mechanical soil disturbance; Hu et al., 2022; Yeates et al., 1993) and environmental pollution (i.e., agrochemicals, microplastics, antibiotics; Kim et al., 2020; Vangheel et al., 2014; Zhu et al., 2021). GCDs may affect microbiome predator communities directly, as well as indirectly through bottom-up effects caused by alterations of the microbiome (Figure 1; Hu et al., 2022; Valencia et al., 2018). Such bottom-up effects are, for example, driven by eutrophication, which stimulates fast-growing microorganisms, including most bacteria, more than slow-growing microorganisms, including most fungi (de Vries et al., 2006). These differential microbiome changes result in increased abundances of bacterivorous compared with fungivorous protists and nematodes (Hu et al., 2022; Shaw et al., 2019; Siebert et al., 2019). However, the consequences of such microbiome-mediated changes in microbiome predator abundances and their resulting impacts on ecosystem functioning remain unexplored.

GCDs may also directly affect the performance and abundance of microbiome predators. In contrast to microbiome-driven changes in microbiome predator communities, direct effects of GCDs on microbiome predator communities may alter their top-down control of soil microorganisms, with consequences for ecosystem functioning (see above and Figure 1). Indeed, such disruptions are likely to take place, as, for example, soil protist communities are more strongly affected by distinct types of environmental pollution and agricultural practices than bacterial and fungal communities (Carley et al., 2020; Zhao et al., 2019; Zhu et al., 2021). Likewise, many nematode taxa show a particularly strong sensitivity to certain GCDs (Wilschut & Geisen, 2021). Especially, drought is a major GCD that alters nematode community composition (Yan et al., 2018), with important implications for nematode top-down control impacts on the microbiome. More knowledge on the direct and indirect impacts of GCDs on microbiome predators and, especially, their consequences for soil functioning must be obtained (Figure 1).

Microbiome predator traits may help to understand their responses to different GCDs. So far, body size has been proven to be the most useful trait to determine and understand microbiome predator responses to global change. As body size is typically strongly associated with longevity and reproduction (Brown, 2004), large-bodied microbiome predators often show a slower recovery than smaller-bodied microbiome predators after environmental disturbances, leading to changes in microbiome predator community composition. For example, large-sized nematode taxa recover more slowly than smaller-sized nematodes after soil disturbances induced by agricultural practices (Ettema & Bongers, 1993). This differential response of large versus small nematodes led to the establishment of several nematode-based indices for soil quality assessments (Du Preez et al., 2022). Larger-sized protists and nematode taxa also respond more negatively to drought than small-sized individuals (Andriuzzi et al., 2020; Geisen et al., 2014). In addition, soil warming has been shown to reduce the average body sizes of key protist and nematode taxa (Knox et al., 2017; Simmons et al., 2009; Tan et al., 2021), corresponding to the Temperature Size Rule (Gibert & DeLong, 2014). However, body size can be confounded by other overlaying response traits as recently shown by Li et al. (2023), who revealed that larger-sized higher trophic groups responded more strongly to differences in environmental parameters than smaller-sized lower trophic groups, but that size did not affect nematode biomass within trophic groups. In addition, other traits that may underlie microbiome predator responses to global changes are highly dependent on the type of GCD involved. For example, mobile protist taxa that depend on water-filled soil pores for their movement may be more negatively affected by drought than surface-bound microbiome predator taxa (Geisen et al., 2014; Wallace, 1968). Another trait underlying differential responses to GCDs is feeding strategy. While feeding on microorganisms, both nematodes and protists risk ingesting microplastics (Fueser et al., 2020; Kanold et al., 2021). In the case of nematodes, bacterivorous nematodes with large mouth cavities are more vulnerable to microplastic ingestion than fungivorous nematodes, which often have a stylet used to puncture fungal hyphae (Fueser et al., 2019). More detailed nematode and protist responses to microplastic pollution and traits underlying this variation remain unknown (Rillig & Bonkowski, 2018). While the impacts of GCDs on individual microbiome predator taxa may be explained by traits, the traits best explaining community-level microbiome predator responses to distinct GCDs remain unknown.

The abovementioned examples highlight that GCDs can affect microbiome predator communities in various ways, and that microbiome predator traits may help to understand their responses to global change. Research on how GCDs affect microbiome predator communities has so far largely focused on examinations of single GCDs (Figure 1). However, soil communities are exposed to multiple simultaneously acting GCDs that together might induce different impacts on GCDs acting in isolation (Rillig et al., 2019; Speißer et al., 2022). Moreover, while it has become evident that microbiome predators may be more sensitive to GCDs than their prey (but see Thakur et al., 2021), the ecological consequences of this higher microbiome predator sensitivity to GCDs have remained unknown. Finally, while traits have been used to some extent to understand microbiome predator responses to GCDs, these responses have so far not been linked to subsequent impacts on the microbiome and soil functioning. Future research on how GCDs affect soil microbiome predator communities should therefore focus on the following questions:

1. How do GCDs affect microbiome predators and their impact on ecosystem functioning?
2. Can microbiome predator traits be used to predict the impacts of GCDs on microbiome predator communities?
3. How do microbiome predator communities and their impacts on the microbiome change ecosystem functioning in response to multiple, simultaneously acting GCDs?

ARE MICROBIOME PREDATORS APPLICABLE SUCH AS IN AGRICULTURE AND IF SO, HOW?

As microbiome predators perform essential functions in soils, they are excellent candidates to be used as biological control agents (BCA) and biostimulants (BS) in agricultural systems (Martins et al., 2022; Nguyen et al., 2023). As such, microbiome predators might be part of the solution to reduce the agricultural application of pesticides and artificial fertilizers. Microbiome predators enhance plant performance of many plant species, including crops such as rice and wheat (Gao et al., 2019; Geisen et al., 2018; Nguyen et al., 2023), through increasing plant phosphorus and nitrogen uptake (Clarholm, 1985; Zheng et al., 2022). If these greenhouse and laboratory results are applicable in the field, fertilization needs for crop production would dramatically decrease. Similarly, pesticide usage could be lowered by the direct or indirect reduction of soil-borne pathogens by microbiome predators (see Introduction section). The wide variety of soil microbiome predator species and traits harbours the opportunity to produce specialized agricultural products for diverse tasks and environments. As microbiome predators are part of a more complex soil microbiome, research on links between the microbiome and microbiome predators can contribute to identifying microbiome predator species of potential use in agriculture (Figure 2). Specific pathogen-preying predators and those that stimulate a pathogen-suppressive microbiome are likely to be found in various systems, but particularly in pathogen-suppressive soils (Guo et al., 2022; Malusà et al., 2021; Vayssier-Taussat et al., 2014). Identification of these main microbiome predator taxa that favourably regulate the microbiome could enhance crop performance and therefore warrants further investigation.

The advantage of microbiome predators as potential stimulators of crop growth compared with currently

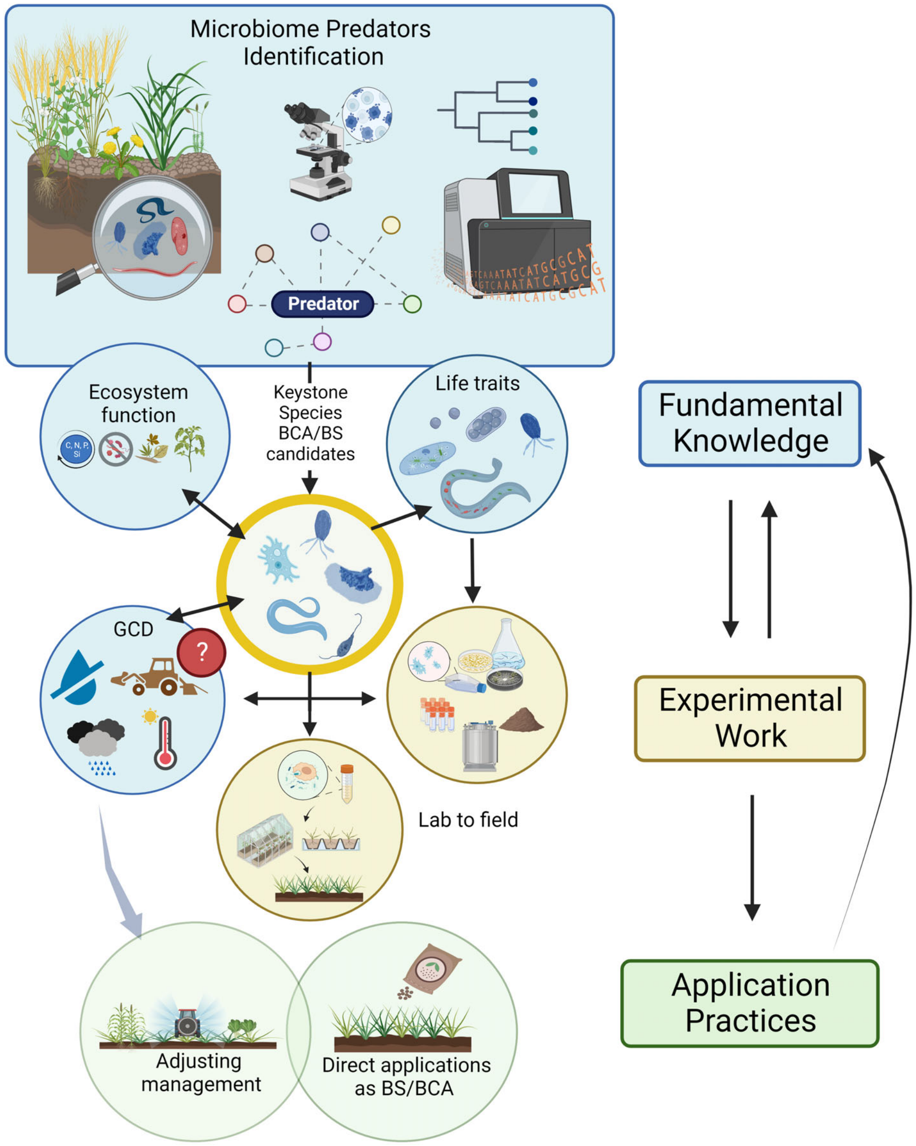

FIGURE 2 The road to the application of soil microbiome predators. To apply predators, it will be essential to increase the fundamental knowledge, about the distribution, occurrence, ecosystem functions, life traits of soil microbiome predators, and how they are impacted by global change drivers (GCDs; blue). With this, keystone taxa can be identified, and their effect on crop performance, as well as culturing and storage characteristics, determined in experimental work (yellow). This experimental work will add to the knowledge about microbiome predator functions as well as how to practically apply them in the field (green). By understanding the impact of GCDs on those keystone taxa, crop performance could also be enhanced by adjusting land management that favours beneficial microbiome predators. BCA, biological control agents; BS, biostimulants.

used BCA/BS in agricultural applications is their overarching top-down control of the entire soil microbiome, rather than providing distinct functions (Asiloglu et al., 2020). This offers further strategies for application, such as co-inoculation of microbiome predators with non-prey plant-beneficial microorganisms (Figure 2), as spatial and resource competition of beneficial microorganisms is reduced (Hawxhurst et al., 2023; Weidner et al., 2017). Indeed, soil microbiome predators might amplify the positive effects of BCA/BS organisms, such as *Trichoderma* and *Bacillus* species (Guo et al., 2022; Mawarda et al., 2022; Xiong et al., 2020), by increasing their dominance and activity in the microbiome (Muller et al., 2013), or by phoresy of biocontrol agents by microbiome predators towards host roots (Hawxhurst et al., 2023). Using microbiome predators in synthetic communities with other microorganisms might therefore represent a boost to already existing BCA and BS products.

In addition to the interaction between microbiome predators and other microorganisms, the interaction between agricultural management and microbiome predator fitness is equally important. Indeed, the effectiveness of inoculum on crop performance is dependent on environmental conditions (Raimi et al., 2021). Agricultural practices and various GCDs alter soil environmental characteristics, such as pH, temperature, and water availability, which can influence soil microorganisms and their predators (Gao et al., 2019; Schwarz et al., 2017; see Conclusion section). Thus, agronomic practices directly affect and stimulate native or applied microbiome predator communities (Asiloglu et al., 2020; Zhao et al., 2020; Zhao & Neher, 2013; Figure 2). Fundamental knowledge, for example, on keystone species and environmental impacts on soil microbiome predators (see Introduction and Conclusion sections) is needed to elucidate the effect of soil management on the native and/or applied soil microbiome predator community, to enhance crop performance through microbiome predator BCA/BS organisms and communities.

Despite their theoretical potential as both BCA and BS products in agricultural systems, the commercial development and agricultural application of microbiome predators are still in their infancy. The use of protists as microbial inoculum has not been widely adopted in the agricultural market. Nevertheless, the first protist-based BS and BCA products have been or are in the process of being established in the market (e.g., Ecostyle ProtoPlus®, Amoéba W. magna C2c Maky; Croze et al., 2021). Currently available nematode-based BCA products, however, focus entirely on entomopathogenic nematodes that control insect pests independent of the soil microbiome (Abd-Elgawad, 2019; Nxitywa & Malan, 2022; Shapiro-Ilan et al., 2023). These existing products can nevertheless considerably advance the development of new microbiome predatory protist and nematode products. This development depends on the selection of applicable microbiome predator species for mass production, field application, and commercial storage, taking into consideration traits like feeding preference, reproduction cycle, and replication rate, as well as their temperature and desiccation tolerance (Lahlali et al., 2022). As these factors are taxon specific, targeted functional research on the life history traits of microbiome predator species is a prerequisite for their application (Nguyen et al., 2023; Figure 2). We pose the following questions to be addressed to successfully apply microbiome predators in agricultural systems:

1. Which microbiome predator species determine a crop-beneficial soil microbiome and where to find them?
2. How to formulate predator-based products for optimal application?
3. How to adjust agricultural management practices enhance the beneficial effects of microbiome predators for crop production?

OUTLOOK AND FUTURE AVENUES

More research is needed to decipher the importance of microbiome predators for plant performance and other ecosystem functions (Figure 1), such as elemental cycling. Most contemporary studies are focusing on a few microbiome predator taxa, neglecting the vast diversity of microbiome predator species and their respective eco-physiological traits involved in ecosystem functioning. Consequently, a broader and more in-depth approach to studying the effects of microbiome predators on multiple ecosystem functions is needed. To do so, it is key to uncover feeding preferences and predation patterns of microbiome predators, the eco-physiological traits underlying such differences, as well as to increase understanding of how a changing community of microbiome predators affects soil functions (Figure 1).

Assessing whether the functions of microbiome predators might be affected by GCDs is key to understanding soil ecosystems under ongoing GCDs. Therefore, future soil ecosystem functioning studies must examine the effects of single and multiple simultaneously acting GCDs with a focus on impacts on microbiome predators (Figure 1), as well as assess whether these impacts can be predicted by microbiome predator traits. At the same time, knowledge of GCD impacts on intact microbiome predator communities (i.e., those in natural systems) may help to identify the factors that suppress microbiome predators and their role in ecosystem functioning in agricultural systems.

Considering their diversity and role in determining ecosystem functioning, as well as their responses to GCDs, research on the applicability of soil microbiome predators in agriculture is needed (Figure 2). It is essential to identify ecological strategies of microbiome predators when engineering or searching for BCA and BS, for the successful establishment and persistence of applied microbiome predator taxa in a native community structure. Also, translating fundamental scientific findings into an applied format warrants extensive research; evaluating the functioning of microbiome predators under lab and greenhouse conditions will help in predicting changes that might follow their introduction into existing soil systems. To optimize microbiome predator success through agricultural management, spatiotemporal analyses on microbiome predators under different field conditions are needed. While the commercial application of soil microbiome predators is still not on the immediate horizon, we believe that soil microbiome predators have major potential for the fast-growing agricultural industry of soil microbial inoculants and urge for their continued investigation and integration into biocontrol and BS application.

CONCLUSIONS

We here summarized current knowledge on the functional importance of microbiome predators in soils and how global change factors might impact those functions and highlighted the potential of microbiome predator application in agricultural systems. All these fields are in their infancy and need substantial work to resolve the more specific questions we defined for each of them. To address these questions and to increase our scientific understanding of soil microbiome predators and their application, we propose a number of steps to be taken in the near future, which include trait-based studies of multiple microbiome predators, impact analyses of GCDs on microbiome predators, and applied studies on microbiome predators. We conclude that microbiome predators should be more regularly studied in soil ecology as their impacts on the soil microbiome might be key for soil functioning, both in natural soils and agricultural ecosystems, now and in the future.

AUTHOR CONTRIBUTIONS

Shunran Hu: Visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Guixin Li:** Visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Alejandro Berlinches de Gea:** Visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Joliese Teunissen:** Visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Stefan Geisen:** Supervision (lead); visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Rutger Wilschut:** Visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Arne Schwelm:** Visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Yuxin Wang:** Visualization (equal); writing—original draft (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Not applicable.

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