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EDITORIAL

The Influence of Beneficial Fungi on Plant–Enemy Interactions and Plant Community Structure

The influence of beneficial fungi on plant–enemy interactions and plant community structure

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Abstract

1. As plant communities respond to global change, there is an urgent need to understand the role of biotic interactions in shaping plant communities' dynamics. Plants simultaneously interact with antagonists and mutualists, and understanding plant community responses to global change requires embracing the complexity of biotic interactions.
2. This cross-journal Special Feature compiled nine research articles and two mini-reviews, each investigating multitrophic interactions, such as plant–insect–mycorrhizae, leaf–mycobiome or seed–mycobiome.
3. We organized these papers around five main themes which highlight the complexity of biotic interactions, their context dependency, the impacts of global change on multitrophic interactions, the use of plant–soil feedback experiments and the consequences of multitrophic interactions for plant communities.
4. *Synthesis*. The articles in this cross-journal Special Feature highlighted important research directions that would help understand the role of beneficial fungi in moderating plant–enemy interactions and plant community structure. In particular, we recommend the need for more experimental studies manipulating multitrophic interactions and geographically replicated experiments to understand the context dependency and the impacts of climate on these complex interactions.

KEYWORDS
beneficial fungi, climate change, context dependency, multitrophic, negative density dependence, plant–enemy interactions, plant–soil feedback

1 | INTRODUCTION

Plant communities are locally regulated by biotic interactions from a diverse pool of organisms that interact with plants both above- and below-ground (Bardgett & Wardle, 2010). Pressure from natural enemies, such as insect herbivores and plant pathogens can result in negative plant–soil feedback and negative density dependence, which may promote plant species coexistence at the community level (recently synthesized in LaManna et al., 2024). In contrast, positive plant–soil feedback, resulting from the accumulation of mutualistic fungi, can lead to competitive exclusion (Tedersoo et al., 2020; Van der Putten et al., 2013). These traditional and broadly accepted concepts, however, are rooted in simple theory where plants only interact with either antagonists or mutualists in isolation. Additionally, studies of plant–soil feedback and negative density dependence traditionally measure the net effects of positive and negative interactions, thereby looking at the combined effects of antagonistic and mutualist interactions without being able to disentangle their distinct, additive and synergistic effects on plant communities (LaManna et al., 2024). This net effect approach prevents us from making accurate predictions on how plant communities will respond to global change as each biotic agent will react differently.

In nature, the combined effects of several factors acting simultaneously are often difficult to disentangle due to potential synergistic or inhibitory effects. Different types of plant natural enemies have inhibitory, synergistic or additive effects on plant communities (Allan & Crawley, 2011; van Ruijven et al., 2005). For example, insects and molluscan herbivores were found to have contrasting impacts on grassland plant diversity in a long-term study (Allan & Crawley, 2011). Similarly, fungal pathogens and insect herbivores often have contrasting effects on plant communities across a range of ecosystems (e.g. Bagchi et al., 2014; Jia et al., 2022). Across trophic levels, nonlinear effects also arise when plants simultaneously interact with beneficial fungi and natural enemies.

Recent advances have highlighted the potential for beneficial fungi to counteract the effects of plant natural enemies and to influence plant community structure (Bachelot et al., 2017; Bennett & Groten, 2022; Neuenkamp et al., 2018; Laliberté et al., 2015; Liang et al., 2021). Yet, the effects of these mutualist fungi are highly context-dependent and remain uncertain in part due to the lack of a clear mechanistic understanding of how mutualistic fungi and natural enemies interact directly and indirectly, and in part due to limited theory on how multitrophic interactions influence plant community structure. These gaps in our mechanistic understanding limit our ability to predict how biotic interactions will shift in the face of global change. Without such knowledge, we will not be able to make accurate predictions about the future of plant communities. This Special Cross-Journal Feature addresses this challenge by exploring how beneficial fungi, natural enemies and plants interact, and the consequences of these interactions for plant community structure.

We have assembled a range of reviews, mini-reviews and research articles that investigate different aspects of mutualist- plant–enemy interactions and their effects on plant communities. These papers investigate multitrophic interactions from the molecular level (Cheng & Yu, 2024; Cibils-Stewart et al., 2024; Fernández et al., 2024) through to the consequences for plant community structure (Bryant & Bever, 2024; Duell et al., 2024; Milici et al., 2024; Pajares-Murgó et al., 2024; Zalamea et al., 2023; Zehr et al., 2024) and plant–microorganism coevolution (Eagar et al., 2024). Here, we provide a brief introduction to the Cross-Journal Special Feature. We identify the major themes covered by the assembled papers (Figure 1) and identify future research directions that would advance the field of ecology by embracing the complexity of biotic interactions.

2 | COMPLEXITY OF ABOVE- AND BELOW-GROUND INTERACTIONS

Plants simultaneously experience above- and below-ground pressure from natural enemies while interacting with several beneficial symbionts, such as arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi and endophytes. The studies compiled in this Cross-Journal Special Feature highlight the complex outcomes that arise from such multitrophic interactions. Although the interactions between mycorrhizal fungi and above-ground herbivory have been extensively studied, especially in grasslands (Bennett et al., 2006; Koricheva et al., 2009), little work has investigated these interactions in the context of both below-ground and above-ground herbivory. Duell et al. (2024) presented an elegant tallgrass mesocosm experiment, manipulating above- and below-ground herbivores and AM symbiosis. Their multitrophic study showed that AM fungi promoted the dominance of C4 grass species, while above- and below-ground herbivory promoted different subdominant prairie species, thereby increasing diversity. Overall, herbivory and AM fungi had interactive effects on plants, whereas herbivory had additive effects. In another multitrophic study presented in the Cross-Journal Special Feature, the authors investigated root and leaf symbionts and how they mediated plant responses to aphids at the molecular level (Cibils-Stewart et al., 2024). As with Duell et al. (2024), the results demonstrated interesting non-additive effects across the multitrophic interactions. While both symbionts helped plant defences against aphids in isolation, the benefit disappeared when the plant was inoculated with both above- and below-ground symbionts due to changes in alkaloid production (Cibils-Stewart et al., 2024). Taken together, these two studies emphasize the need for more multitrophic above- and below-ground studies.

However, multitrophic studies do not need to integrate above- and below-ground levels to provide new insights on the biotic controls of plant communities. Pajares-Murgó et al. (2024) demonstrated how even within the phyllosphere complex, multitrophic antagonistic and beneficial interactions can influence plant communities. In this study, the authors combined data from fungal communities of the phyllosphere and plant recruitment to investigate the roles of phyllosphere composition on sapling recruitment. As expected, similar pathogen composition between saplings and canopy trees were associated with low recruitment probability. In contrast, diversity in epiphytes or saprotrophs resulted in a high recruitment probability. Together, these results point towards the importance of the phyllosphere fungi in plant community assembly (Pajares-Murgó et al., 2024).

3 | CONTEXT DEPENDENCY OF PLANT-BIOTIC INTERACTIONS

Plant–microbe interactions are characterized by strong context dependency and this theme is omnipresent in our Cross-Journal Special Feature. It has long been recognized in plant pathology that the outcome of plant–pathogen interactions depends critically on environmental conditions, perhaps best encapsulated by Stevens' (1960) concept of the disease triangle. The outcome of plant–symbiont interactions can also change dramatically with

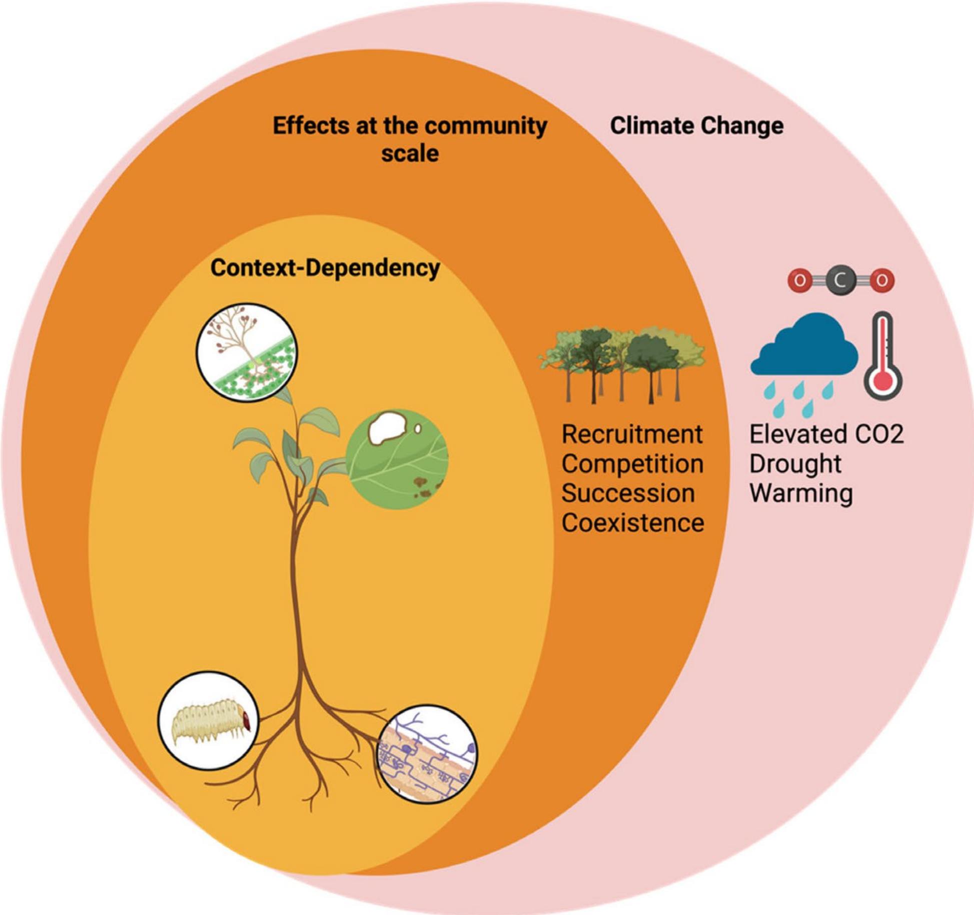

FIGURE 1 Themes highlighted in the special feature emphasizing (1) the complexity of non-additive biotic interactions that change with context, (2) the consequences for plant communities and (3) the role of climate change in modulating the impacts of biotic interactions. This figure was done with BioRender.

environmental conditions (Johnson & Graham, 2013). In this Cross-Journal Special Feature, Cheng and Yu (2024) presented new tools to study host–pathogen interactions, Fernández et al. (2024) highlighted new dimensions of this context dependency that arise with the timing of herbivory, and Cibils-Stewart et al. (2024) demonstrated how multitrophic interactions influence the accumulation of plant secondary compounds.

Ecologists have recognized how the effects of AM fungi change with soil resources (Hoeksema et al., 2010; Johnson & Graham, 2013) and successional status of the plants (Bachelot et al., 2018; Janos, 1980; Koziol & Bever, 2019) in grasslands (Koziol & Bever, 2019) and tropical forests (Bachelot et al., 2018). However, Bryant and Bever (2024) introduced a new theme centred on how climate might modulate this context dependency. Using a large greenhouse experiment, the authors found that the importance of AM fungi for succession would increase in future climate scenarios that have more frequent drought.

Understanding how climate alters the context dependency of plant–enemy–mutualist interactions should be an important research goal of plant community ecologists. The disease triangle is being redefined by climate change (Roussin-Léveillée et al., 2024) in the same way Bryant and Bever (2024) showed how altered climate might shift our traditional expectations of context dependency in plant–mycorrhizal interactions. As we will discuss next, studies in this cross-journal special feature investigated how climate change influences the context dependency of both plant enemies and mutualists, which we hope will prime this field for further development.

4 | CLIMATE CHANGE MODULATES MULTITROPHIC PLANT INTERACTIONS

Another dominant theme in this Cross-Journal Special Feature is how climate change will modulate multitrophic plant interactions. Together these studies share the same message: future climate will change biotic interactions in ways that will strongly reshape plant communities (Blois et al., 2013).

Two studies showed the impacts of altered precipitation on biotic interactions and their consequences for plant communities. For example, Milici et al. (2024) found that under drought in Panama, negative plant–soil feedback disappeared (which could be associated with a decrease in plant diversity). Fungal pathogens' performance is thought to decrease with decreasing precipitation (Bachelot et al., 2016; Gillett, 1962; Givnish, 1999), which would explain a weakening of negative density-dependent effects in drought conditions. However, this result contrasts with a recent analysis of foliar pathogen damage incidence in Panama along a precipitation gradient (Milici et al., 2024). In this study, foliar pathogen damage incidence was higher in dry sites. Discrepancies could arise as environmental change alters various parts of fungal life cycles in different ways (e.g. precipitation may enhance dispersal of waterborne spores but inhibit aerial spore dispersal), with contrasting impacts on above- and below-ground plant–microbe interactions. As a result, predicting the implications of global change for coexistence mechanisms requires an integration of impacts on the whole plant microbiome. A second study presented in this special feature emphasized the role of precipitation; in a temperate grassland, drought enhanced the importance of AM fungi for successional dynamics (Bryant & Bever, 2024). Specifically, late successional plant species, which are more responsive to AM fungi (Bachelot et al., 2018; Janos, 1980; Koziol & Bever, 2019), tended to become increasingly responsive to AM fungi under low water conditions (Bryant & Bever, 2024). Together, these two studies point to a decreasing role of fungal pathogens and an increasing role of AM fungi under low water conditions, suggesting an increase in the relative importance of positive plant–soil feedback compared with negative plant–soil feedback, which could have strong consequences for plant communities (Bachelot et al., 2020).

Finally, a mini-review of plant-EM–herbivory interactions under elevated CO_2 suggested that EM fungi might become increasingly important in mediating plant responses to herbivory in future climate (Zehr et al., 2024). This mini-review compiled the existing results from elevated CO_2 experiments and highlighted emerging patterns. Previous reviews have already shown that herbivory will likely increase under elevated CO_2 due to higher insect metabolism, higher consumption rates due to lower leaf quality and lower leaf defence (e.g. Hunter, 2001; Zavala et al., 2013). Zehr et al.'s (2024) mini-review went one step further and investigated changes in herbivory in the context of plant–mycorrhizal fungal interactions. Throughout the review, the authors emphasized the need for more studies as results vary greatly across published datasets. Nevertheless, the existing data suggested that under elevated CO_2, it might be increasingly important to consider how plant–mycorrhizal fungal interactions will modulate plant–insect interactions.

5 | PLANT–SOIL FEEDBACK AS A TOOL TO UNDERSTAND CONTEXT DEPENDENCY

By emphasizing the complexity of biotic interactions, the multitrophic studies published in this Cross-Journal Special Feature highlighted the daunting task that ecologists face when trying to predict how plant communities might respond to environmental change. Understanding the context dependency of the effects of biotic interactions is key to making future predictions (Araújo & Luoto, 2007; Lai et al., 2024; Van der Putten et al., 2010). Plant–soil feedback studies can provide valuable insights about general patterns in how the overall balance of the mutualistic and antagonistic effects might shift in response to environmental changes. For example, Milici et al. (2024) used a plant–soil feedback experiment with six shade-tolerant tree species in Panama to show that under reduced soil moisture, plant–soil microbe interactions shifted from negative to neutral, which weakens an important mechanism promoting plant diversity. The mini-review by Eagar et al. (2024) provided clear criteria for when to expect positive and negative plant–soil feedback to arise depending on mycorrhizal traits. In particular, the authors contrasted the general association between AM fungi and negative plant–soil feedback (as in Milici et al., 2024) with the association between EM fungi and positive plant–soil feedback. Finally, the authors provided new directions for how climate and evolution might influence these dynamics.

6 | MULTITROPHIC INTERACTIONS SHAPE PLANT COMMUNITIES

The overarching theme of this Cross-Journal Special Feature was to highlight how multitrophic interactions shape plant communities. Competition and predation have been extensively studied in the context of plant community structure (e.g. Sih et al., 1985; Tilman, 1982). Similarly, mutualism has been proposed as an important driver of plant community dynamics (Bennett et al., 2017; Klironomos, 2002; Tedersoo et al., 2020). Less attention has been placed on disentangling the role of multitrophic interactions in shaping plant communities (LaManna et al., 2024). In this Cross-Journal Special Feature, one study showed that complex multitrophic interactions can influence plant community structure (Pajares-Murgó et al., 2024). In this study, the authors focused on the fungal communities of the phyllosphere and their contribution to plant recruitment. As expected, fungal pathogens had a negative effect on plant recruitment (Connell, 1971; Janzen, 1970) but the community of mutualist fungi was also an important driver of plant recruitment by enhancing recruitment in the sapling bank of species with similar epiphyte communities (Pajares-Murgó et al., 2024).

Plant recruitment starts with successful germination. The traditional Janzen and Connell hypothesis proposes that seed natural enemies are responsible for the maintenance of local plant diversity (Connell, 1971; Janzen, 1970). In particular, soil-borne fungal pathogens are responsible for high seed mortality in tropical forests (Dalling et al., 1998). Recently, seeds of *Cecropia* species were found to rely on protection from soil-borne fungi (Dalling et al., 2020; Zalamea et al., 2021). In this special feature, Zalamea et al. (2023) investigated the seed fungal communities of two additional abundant pioneer tree species on Barro Colorado Island (Panama). The authors found that the composition of fungal assemblages did not differ significantly between viable and inviable seeds, even though the two pioneer species harboured distinct fungal communities. The authors concluded that more work was needed to investigate the functional roles of the isolated non-lethal fungi on viable seeds with potential roles of microbial-induced defences in seeds.

Besides plant recruitment, studies in this special feature also investigated the role of multitrophic interactions on plant community structure (Duell et al., 2024) and succession (Bryant & Bever, 2024). Duell et al. (2024) used a mesocosm experiment to investigate plant community responses to AM fungi inoculation on above- and below-ground herbivory. This grassland study highlighted the clear roles of both antagonistic and mutualistic interactions in shaping grassland communities (Duell et al., 2024). The other grassland study in this special feature focused on the role of mycorrhizal fungi in plant community succession in the face of climate change (Bryant & Bever, 2024), but the authors did not investigate antagonistic interactions with plant natural enemies. Nonetheless, this study showed some important results in how climate change might modulate the roles of mycorrhizal fungi in plant community succession, emphasizing the need for more studies investigating how these biotic interactions shape plant communities now and in the context of climate change.

7 | FUTURE DIRECTIONS

Understanding the response of plant communities to global environmental change requires ecologists to embrace the complexity of multitrophic interactions. The papers compiled in this special feature demonstrate how biotic interactions might have unexpected effects when acting jointly on plant communities, and their roles might be redefined by environmental change. We highlight two major directions that deserve immediate attention.

First, as pointed out by Cibils-Stewart et al. (2024), Duell et al. (2024) and Zehr et al. (2024), multitrophic studies manipulating both above- and below-ground biotic interactions are needed to grasp their combined roles in shaping plant communities. We recognize that this might be a daunting task in many ecosystems, yet tools are continuously being developed to make this goal achievable. For example, within this special feature, a Cheng and Yu (2024) proposed a new tool to investigate the specificity of plant–fungi interactions in tropical forests (Cheng & Yu, 2024). Understanding the specificity of plant–fungi interactions, both above- and below-ground, is important as host specificity of these biotic interactions influences their potential to influence community scale patterns (Bruijning et al., 2024).

Second, the roles of biotic interactions are being redefined by global environmental change. This is something illustrated by several data studies (Bryant & Bever, 2024; Milici et al., 2024) in this special feature and summarized by a mini-review (Zehr et al., 2024). There is an urgent need to understand how biotic interactions are changing and what the consequences are for plant communities at the global scale. To best address this need, we call for large-scale distributed experiments manipulating biotic interactions and climate.

AUTHOR CONTRIBUTIONS

Benedicte Bachelot, Robert Bagchi and Sunshine A. Van Bael jointly conceived and wrote the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

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This paper has no data.

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