Ecology and management perspectives in arthropod–fungal associations

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Abstract

Fungal interactions with arthropods remain underexplored despite their abundance and ecological importance. Arthropod-associated fungal parasites and pathogens span a wide range of strategies in their interactions with hosts. At one end of the spectrum are obligate ectobionts and ectoparasites, such as the Laboulbeniales, which depend entirely on living hosts to complete their life cycle. At the other end, highly specialized entomopathogenic fungi, including *Ophiocordyceps unilateralis* and *Pandora neoaphidis*, kill their hosts to reproduce and disperse. Others, such as *Beauveria bassiana* and *Metarhizium brunneum*, are more facultative and generalist, capable of infecting a broad range of hosts while also persisting as saprotrophs or endophytes in the absence of suitable hosts. These associations influence arthropod population dynamics, community structure, and ecosystem processes, while also offering opportunities for applied biological control. This chapter reviews current knowledge on fungal parasites and pathogens of arthropods. We discuss host dependence, specificity, and behavioral manipulation, and abiotic drivers shaping infection dynamics and fungal persistence. We also identify key research challenges, from clarifying lifestyle transitions to assessing community-level impacts, and propose interdisciplinary approaches to advance understanding. Together, these insights underscore the ecological and applied significance of arthropod–fungal associations. We hope that this review will encourage more researchers to engage with the rich and largely untapped diversity of arthropod–fungal associations.

Introduction

Fungi represent one of the most diverse groups of eukaryotic organisms on Earth with an estimated 2.5 million species, of which only a fraction have been formally described (Niskanen *et al.*, 2023). This diversity is reflected not only in taxonomy but also in ecological strategies: fungi recycle organic matter as saprotrophs, form mutualistic associations such as mycorrhizae and lichens, and exploit living organisms as parasites and pathogens (Piepenbring *et al.*, 2016; Runnel *et al.*, 2025; Willis, 2018). Through these strategies, fungi interact with virtually all other forms of life, including plants, animals, protists, bacteria, and even other fungi (Naranjo-Ortiz *et al.*, 2019; Weiland-Bräuer, 2021; Bahram and Netherway, 2022; Costa *et al.*, 2024). While plant–fungal interactions have received considerable attention due to their economic and ecological importance, fungal associations with animals have been comparatively neglected. As an example, only 66 of 1882 fungal species newly described in 2019 were animal-associated (Cheek *et al.*, 2020). This imbalance is striking given that a substantial proportion of these interactions involve arthropods as hosts.

Arthropods represent the most species-rich group of animals, with estimates up to 6 million species worldwide (Chakravarthy *et al.*, 2016). They provide a vast and varied set of habitats for fungi, and indeed thousands of fungal species are known to parasitize arthropods (Mueller and Schmit, 2007). Yet, our knowledge of the true diversity, ecological roles, and evolutionary dynamics of these associations remains fragmentary. Closing these gaps is not only essential for understanding fungal diversity and evolutionary relationships but also has practical implications for conservation and the development of sustainable biological control strategies.

The aim of this chapter is therefore to explore fungal parasites and pathogens associated with arthropods, with a particular focus on the diseases they cause in both natural and managed ecosystems. We further examine how environmental conditions shape the dynamics of these diseases. By synthesizing current knowledge, we highlight the ecological significance of arthropod–fungal interactions and point to avenues for future research.

Definitions

Before delving into the ecological and evolutionary dynamics of fungal diseases in ecosystems, it is important to establish clear working definitions of the terms we use. The terminology surrounding parasites and pathogens is not uniform across disciplines, and interpretations often vary depending on whether one studies mycology, invertebrate pathology, or the broader field of parasitology. Here, we follow Kaishian *et al.* (2024) and others in distinguishing between parasites and pathogens. Parasites are defined as multicellular organisms that live at the expense of a single host, reducing its fitness but not directly causing death (sensu Haelewaters *et al.*, 2017). Pathogens, in contrast, are microorganisms capable of producing disease under normal conditions of host resistance, and they rarely persist in close association with the host without producing disease (sensu Onstad *et al.*, 2006). From this perspective, parasitism encompasses a spectrum of associations with varying impacts on host fitness, whereas pathogenicity implies a clear disruption of host health and, in many cases, eventual death.

In the case of fungi, the term entomopathogenic fungi (EPF) is widely used to describe fungal species that infect and cause disease in insects. These fungi occupy a central role in regulating insect populations in nature and in applied biological control. The first to reveal a pathogenic association between fungi and insects was Agostino Bassi, who demonstrated in 1834 that *Beauveria bassiana* (Sordariomycetes: Hypocreales) was the causal agent of white muscardine disease in silkworms (Lepidoptera: Bombycidae: *Bombyx mori*) (Latgé and Papierok, 1988; Mazzarello *et al.*, 2013). This discovery marked one of the earliest recognitions of a microorganism as the cause of an infectious disease, predating the germ theory of Pasteur and Koch. A few decades later, Louis Pasteur himself explored the use of "hyphomycetes" for aphid control (Latgé and Papierok, 1988), setting the stage for the applied study of EPF.

The boundaries between parasites and pathogens are not always clear. Many fungi exhibit characteristics that place them in a gray zone. For example, *Hesperomyces harmoniae* (Laboulbeniomycetes: Laboulbeniales) is usually regarded as an ectoparasite of ladybirds (Coleoptera: Coccinellidae), but laboratory bioassays have shown that infection increases host mortality (Haelewaters *et al.*, 2020). This suggests that *He. harmoniae* can exert pathogenic effects, but the ecological conditions under which it might behave as an opportunistic pathogen require further study. A similar ambiguity is found in members of Harpellales (Harpellomycetes), a group of gut-dwelling fungi associated with aquatic insect larvae. Species of *Smittium* (Harpellales: Harpellaceae) typically inhabit the digestive tracts of dipteran larvae and are considered commensals or mutualists. However, *S. morbosum* negatively affects host development and survival, suggesting a shift toward pathogenicity under certain conditions (Sweeney 1981, 2008; Wang *et al.*, 2019).

These cases highlight that trophic mode may shift along a parasite–pathogen continuum depending on host and environmental context, but so far these shifts have only been documented for a few well-studied species. They also illustrate that the definitions for parasites and pathogens can be fluid rather than strictly distinct. While many mycologists treat pathogenic associations as a subset of parasitic ones, invertebrate pathology often maintains a stronger conceptual boundary between the two (Onstad *et al.*, 2006; Kaishian *et al.*, 2024). What is generally agreed upon is that fungal pathogens may directly kill their host, whereas parasites may persist without causing death. After parasite infection, the host's immune system is weakened, making it more susceptible to secondary infection, for example by a microbial pathogen, that may ultimately kill the host. Yet, in practice, disciplinary perspectives influence how definitions are applied.

Finally, fungal interactions with arthropods cannot be fully understood without recognizing that they exist alongside a continuum of other relationships, including mutualisms. Some fungi form beneficial associations with insects, such as nutritional symbioses in gut fungi or in farming systems of ants, termites, and beetles (Mueller and Gerardo, 2002; Blackwell *et al.*, 2007). Some fungi, as a group, can occupy a range on the spectrum of symbiosis. An example are the Laboulbeniales, of which some increase host mortality (Haelewaters *et al.*, 2020; Szentivanyi *et al.*, 2021) and others protect against entomopathogenic fungi (Konrad *et al.*, 2015). Yet other fungi can be mutualists and pathogens simultaneously. Endophytic insect-pathogenic fungi live inside the tissues of their plant host without causing any symptoms but they infect and kill plant insect pests (Branine *et al.*, 2019). In another example, *Metarhizium* isolated from paddy soils exhibits a remarkable dual functionality: it promotes plant growth while simultaneously acting as a biocontrol agent against the brown planthopper, one of the most important pests of rice (Kobmoo *et al.*, 2025). These different strategies by which fungi exploit or collaborate with a multitude of hosts underscores the diversity and ecological complexity of fungal life histories.

Significant impacts in natural and managed ecosystems

Biodiversity and natural associations

Fungi associated with arthropods represent an important but underappreciated component of biodiversity. These interactions span a wide spectrum, from parasitism to more ambiguous relationships that remain difficult to classify. For instance, some fungal–arthropod interactions are well documented and clearly circumscribed, while others are poorly characterized or undefined, such as those highlighted in recent databases of fungal associations (De Wint *et al.*, 2024).

In natural ecosystems, the host range of EPF varies widely. The vast majority species within Entomophthoromycotina (Zoopagomycota) (76%) are highly host specific; they infect species in a single arthropod family (Sacco and Hajek, 2023). However, some species exhibit broad host ranges, such as *Zoophthora radicans* (Entomophthorales) that has been reported from Diptera, Hemiptera, Hymenoptera, and Lepidoptera (Keller, 1991). A similar range of host specificity patterns is observed within the genera *Cordyceps* and *Ophiocordyceps* (Sordariomycetes: Hypocreales). Many species are highly specialized. For example, *Ophiocordyceps unilateralis* sensu lato (s.l.), the famous "zombie-ant fungus", is a complex of species that only infect ants in subfamily Formicinae, tribe Camponotini (except *O. cephalotiphila* on ants in Myrmicinae: Attini), and multiple species within the complex are specific to one or two ant species (Kobmoo *et al.*, 2012; Araujo *et al.*, 2018; Ballesteros-Aguirre *et al.*, 2025). On the other hand, *Cordyceps militaris* is most commonly recorded from Lepidoptera, but other hosts include Coleoptera, Diptera, and Hymenoptera (Shrestha *et al.*, 2012; Wang *et al.*, 2023). However, such broad host ranges should be treated with caution; it is very well possible that fungi identified as *C. militaris* from hosts other than Lepidoptera may represent different species, as is seen in Laboulbeniales (see below) but also plant-pathogenic fungi (Kruse *et al.*, 2018).

Most Laboulbeniales are highly host specific (Haelewaters *et al.*, 2021). Some species have wide host ranges but there is increasing evidence that at least some of the species thought to have a wide host range are actually complexes of multiple species segregated by host (e.g., Haelewaters *et al.*, 2018; Van Caenegem *et al.*, 2023). Finally, the occurrence of species on accidental and occasional hosts that are phylogenetically distant from the main host (in different orders or even subphyla), can be explained by shared micro-habitats such as ant nests (Blum, 1934; Pfliegler *et al.*, 2016; Parmentier *et al.*, 2026) and subterranean caves (Reboleira *et al.*, 2017). Accidental transmissions may have played an important role in reproductive isolation and speciation of Laboulbeniales (De Kesel and Haelewaters, 2014).

Taken together, these cases highlight that arthropod-associated fungi exhibit a striking continuum of host associations, from generalist to extreme specialization. This variation reflects the interplay of ecological opportunities, evolutionary history, and the biology of both fungi and their hosts. Crucially, differences in host range also shape the ecological impacts of these fungi: specialists may act as natural regulators of single host populations, whereas generalists can influence multiple species simultaneously, with cascading effects on community structure and ecosystem dynamics. In both natural and managed ecosystems, therefore, the diversity of arthropod–fungal associations is not only a question of taxonomy but also a driver of ecological processes, from the regulation of insect populations to shifts in biodiversity at larger scales.

Managed ecosystems and biological control

In managed ecosystems, arthropod-associated fungi play a central role in biological control. Intentional introductions of EPF as biocontrol agents have been pursued for decades (Eilenberg *et al.*, 2001). While often effective against target pests, such interventions also raise ecological questions. The release of EPF to suppress pests may inadvertently impact non-target arthropods, with cascading effects on local biodiversity (Cappa *et al.*, 2024; Wang *et al.*, 2024). Careful assessment of these broader impacts is therefore essential when considering fungi for integrated pest management.

The concept of biological control itself has been interpreted differently across disciplines. According to the widely used definition of Eilenberg *et al.* (2001), biological control is “the use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be.” This definition recognizes four strategies:

- Classical biological control – the long-term introduction and establishment of an exotic antagonist to control an introduced pest.
- Conservation biological control – the protection and enhancement of naturally occurring antagonists, often through selective pesticide use and habitat management.
- Inoculation biological control – the intentional release of an antagonist with the expectation that it will establish and provide medium-term control.
- Inundation biological control – short-term control based on mass release of an antagonist without persistence of its progeny.

Although this framework is broadly applied, it has not been universally accepted. Plant protection specialists, for instance, sometimes use alternative terminologies or focus on different aspects. Recent work has highlighted these nuances and underscores the importance of reconciling perspectives across applied fields (Wyckhuys *et al.*, 2024).

Concrete examples highlight both the promise and complexity of EPF in managed landscapes. *Metarhizium anisopliae* s.l. (Sordariomycetes: Hypocreales) has been successfully employed in locust and grasshopper control programs across Africa and Asia, reducing crop damage without heavy reliance on chemical pesticides (Lomer *et al.*, 2001). Also *Beauveria bassiana* has been widely tested against forest pests, such as bark beetles and defoliating caterpillars. However, results vary depending on environmental conditions and application methods (Hajek and St. Leger, 1994). At the same time, concerns persist about unintended effects: laboratory and field studies have demonstrated that non-target insects, including predators and parasitoids, can be susceptible to infection under specific conditions (Meyling and Eilenberg, 2007). Additionally, pollinators such as honeybees (*Apis mellifera*), bumblebees (*Bombus terrestris*), solitary bees (*Osmia bicornis*), and stingless bees (*Scaptotrigona depilis*, *Tetragonisca angustula*) can experience sublethal effects or increased mortality when exposed to EPF, depending on factors like exposure route, spore concentration, and the environment (Leite *et al.*, 2022, Wueppenhorst *et al.*, 2024; Biryol *et al.*, 2025). These examples underscore both the ecological utility and risks associated with introducing fungal antagonists into complex ecosystems.

The same dynamic has been reported for Laboulbeniales. *Hesperomyces harmoniae* has been explored as a candidate biological control agent of its main host, the globally invasive ladybird *Harmonia axyridis* (Haelewaters *et al.*, 2020; de Groot and Haelewaters, 2022; de Groot *et al.*, 2024). Recent experimental work, however, shows that *He. harmoniae* can also infect non-target ladybirds, including the European-native species *Adalia bipunctata*, *Coccinella septempunctata*, *Myzia oblongoguttata*, and the closely related *Ha. quadripunctata* (M.D. de Groot & D. Hessmann, unpublished data), highlighting the risk of non-target effects. Together with studies on environmental factors shaping parasitism by *He. harmoniae* (e.g., de Groot *et al.*, 2026), these findings underscore the need for careful risk assessment before integrating parasite–host–environment interactions into management strategies.

Conservation and ecosystem comparisons

Comparisons between natural and managed ecosystems further emphasize the dual role of EPF. In natural systems, these fungi help regulate insect populations and maintain ecological balance (Roy *et al.*, 2006). In managed systems, conservation biological control strategies aim to harness these natural processes, for example by preserving non-crop habitats that favor fungal antagonists (Pell *et al.*, 2010). Such practices illustrate the convergence of biodiversity conservation and pest management, where fungi act simultaneously as regulators of insect populations and as practical tools for sustainable agriculture.

Biotic and abiotic factors

Host dependence: obligate and facultative strategies

Fungal infection dynamics in arthropods are largely determined by host-related traits, especially host reliance and adaptation (**Fig. 1**). Fungi exploit arthropod hosts for nutrients, habitat, transmission, and reproduction, although the degree of host dependence varies greatly across lineages. Laboulbeniales are obligate ectobionts and ectoparasites, entirely reliant on living hosts to complete their life cycle (Haelewaters *et al.*, 2022). Most Entomophthorales (e.g., *Pandora neoaphidis*) are also obligate pathogens, requiring living hosts for growth and reproduction (Hajek and St. Leger, 1994; Goettel *et al.*, 2005; Ben Fekih *et al.*, 2019; Eilenberg *et al.*, 2019). In contrast, many Hypocreales, such as *Beauveria bassiana* and *Metarhizium brunneum*, are facultative pathogens, i.e., they can infect insect hosts to reproduce and disperse but are also capable of persisting as saprotrophs in soil or as endophytes within plants (Hajek and St. Leger, 1994; Inglis *et al.*, 2001; Butt *et al.*, 2016).

Behavioral manipulation

Some specialized fungi manipulate host behavior to enhance transmission and spore dispersal. Such manipulations are strongly influenced by host morphology and ecology and are rarely found in generalist fungi (Andersen *et al.*, 2009; Hughes *et al.*, 2011; Fredericksen *et al.*, 2017; Lovett *et al.*, 2020). Species in Clavicipitaceae, Cordycipitaceae, and Ophiocordycipitaceae induce infected arthropods to adopt behaviors that enhance fungal transmission. For example, *Ophiocordyceps unilateralis* s.l. and *O. humbertii* s.l. induce a "death grip," where ants or wasps latch onto plant substrates with their mandibles, stabilizing the host after death. The fungal mycelium fuses with muscle tissue to prevent release. Similarly, Entomophthorales members manipulate aphids and flies to die in elevated positions, a phenomenon known as "summit disease," which optimizes cadaver positioning for conidial dispersal (Roy *et al.*, 2006). Recent studies have further elucidated the mechanisms and host-pathogen interactions involved in summit disease, revealing that fungal pathogens induce changes in host behavior, nervous system modulation, and physiological alterations to promote climbing and fixated death on elevated substrates (Elya and De Fine Licht, 2021; Masoudi *et al.*, 2024). Infected flies, for example, exhibit an unsteady gait and leg spasms leading to substrate-hugging behavior, which ensures cadaver stability and effective spore release (Elya *et al.*, 2018; Elya and De Fine Licht, 2021). In addition, the fungus releases volatiles that lure healthy males into mating with female fly cadavers, thereby increasing chances of infection (Naundrup *et al.*, 2022). Such manipulations represent convergent evolution of host control, occurring in both specialist and some generalist lineages, although the precision and complexity of the behavior are usually higher in host-specific fungi (de Bekker *et al.*, 2014).

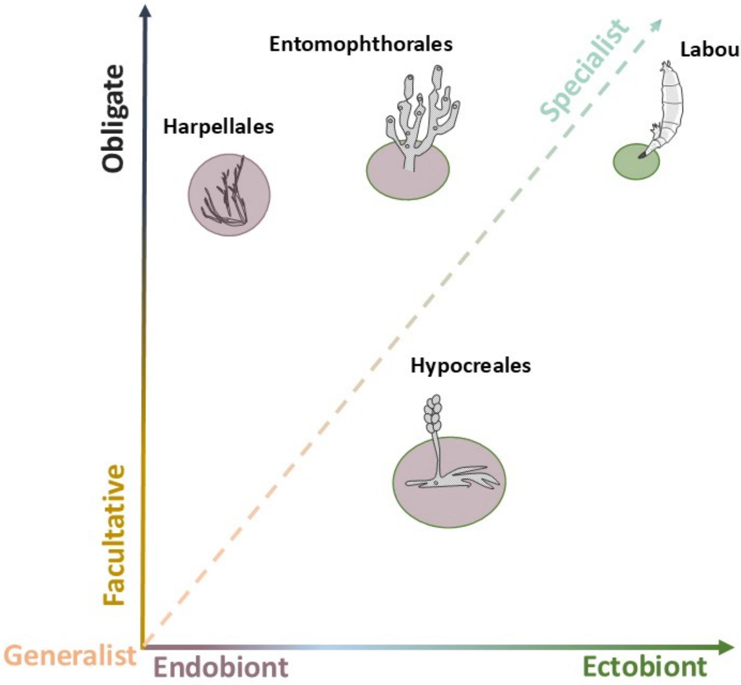

Figure 1: Three-dimensional conceptual figure illustrating the biological diversity of fungi involved in interactions with arthropods. The figure positions fungal lifestyles within a framework defined by (1) host dependence (from facultative to obligate), (2) host range (from generalist to specialist), and (3) symbiotic position (from endobiont to ectobiont). Facultative pathogens (e.g., Hypocreales) occupy regions of lower host dependence, while obligate pathogens (e.g., most Entomophthorales) and ectobiont parasites (e.g., Laboulbeniales) cluster toward the specialist end of the spectrum. Morphological differences illustrate symbiotic positioning: Entomophthorales and Hypocreales show mycelial outgrowths extending from internal (endobiont) structures to external projections, Laboulbeniales develop purely ectobiont thalli, and Harpellales remain entirely endobiont with no external fungal outgrowth.

Transmission and host availability

The ability of entomopathogenic fungi to persist and spread depends not only on their interactions with individual hosts but also on how they manage transmission across host populations and endure periods when suitable hosts are scarce. Laboratory bioassays simulating field conditions have shown that fungi sporulating on conspecific cadavers produce higher virulence and faster transmission to conspecific hosts than heterospecific cadavers, highlighting the ecological importance of host–pathogen specificity (Ben Fekih *et al.*, 2019). Beyond such direct cycles, fungi may spend part of their life cycle as spores that must encounter hosts, either directly (e.g., during mating of hosts in the case of Laboulbeniales) (Haelewaters *et al.*, 2012; Fiedler and Nedvěd, 2019) or via environmental media such as air or water (e.g., *Ophiocordyceps* and *Aschersonia*/*Hypocrella*) (Shang *et al.*, 2015; Luangsa-Ard *et al.*, 2018). Some species persist in environmental reservoirs, remaining dormant until susceptible hosts appear, thereby bridging temporal gaps in host availability (Evans, 1989; Niu *et al.*, 2019; Haelewaters *et al.*, 2020). For instance, *Ophiocordyceps sinensis,* which infects Lepidoptera larvae, can persist endophytically in plants, awaiting larval feeding to initiate infection (Wang *et al.*, 2020). The mobility of arthropod hosts adds further complexity, contrasting with plant–pathogen systems where hosts are sessile. Together, these strategies illustrate how the reliance of fungi on host availability shapes not only their immediate transmission success but also their long-term persistence within dynamic arthropod communities.

Climatic and microenvironment

Environmental conditions strongly influence fungal infection dynamics. Moisture and humidity are critical for spore adhesion, germination, and fruiting body formation, though effects vary among species and study systems (Inglis *et al.*, 2001; Haelewaters *et al.*, 2020; de Groot *et al.*, 2026). Some fungi rely on microhabitats with narrow humidity ranges to maximize infection success, while others tolerate broader conditions. Temperature also regulates fungal growth, virulence, and sporulation, with species- and strain-specific optima. For example, *Beauveria bassiana* and *Metarhizium anisopliae* s.l. exhibit distinct thermal optima for infection (Fargues *et al.*, 1997; Bugeme *et al.*, 2008). Such variations highlight the importance of local climate conditions in shaping fungal ecology and determining when and where infections can occur.

Land use and habitat context

Land use fundamentally shapes the distribution and ecology of arthropod-associated fungi. Intensive agricultural practices often reduce the diversity and abundance of EPF through the use of pesticides, soil disturbance, and habitat simplification, limiting their interactions with potential hosts (Ali-Shtayeh *et al.*, 2003; Steinwender *et al.*, 2014; Meyling and Eilenberg, 2007; Ramos *et al.*, 2017). In contrast, semi-natural habitats and organically managed systems can act as reservoirs, supporting both arthropods and their associated fungi, and facilitating spillover between managed and unmanaged landscapes (Bidochka *et al.*, 2001; Meyling *et al.*, 2011).

Shifts in host availability, including the arrival of invasive or non-native species, further shape these dynamics. Evidence from plant-associated systems shows that host identity, geography, and climate jointly structure fungal communities (Franić *et al.*, 2023), suggesting similar processes operate in arthropod-associated fungi. For example, hypocrealean EPF are more frequently isolated from organic than conventional orchards, reflecting the role of reduced pesticide use and greater habitat complexity in promoting fungal occurrence (Tkaczuk *et al.*, 2019). Forest soils, and in particular leaf litter, likewise harbor diverse and functionally important fungal populations that contribute to regulating arthropod communities (Majchrowska-Safaryan and Tkaczuk, 2021).

These landscape-level dynamics illustrate that land use affects not only the distribution of EPF but also their ecological functions, including host regulation, non-target interactions, and applications in biological control (Goettel *et al.*, 2005). Integrating land-use perspectives is therefore critical to understanding and predicting arthropod–fungal associations in both natural and managed ecosystems.

Challenges and future directions

Building on our understanding of how biotic and abiotic factors shape arthropod–fungal interactions, several critical knowledge gaps remain, offering opportunities for research over the next 5–10 years. Efforts should focus on clarifying how environmental conditions, host traits, and fungal biology influence these interactions, with implications for population regulation, biodiversity conservation, and sustainable pest management. The issues outlined below represent just a subset of the many compelling research priorities in arthropod–fungal ecology, underscoring the breadth of work still needed in the field.

1. Investigate how microhabitat conditions influence the efficacy of fungal infections on arthropod hosts, to enhance the regulation of natural populations.

2. Understand how invasive and native arthropods respond to fungal infection under field conditions, and how these responses shape infection dynamics. This will help to design pest management strategies that stabilize predator communities and maximize control efficacy.
3. Identify environmental factors that trigger a possible fungal lifestyle transition will be essential for predicting ecological outcomes and minimizing unintended impacts.
4. Construct a trait-based framework to link life history traits of hosts (e.g., diet, phenology, body size) with infection by fungal parasites and pathogens.
5. Conduct integrative studies to explore how fungal interactions intersect with broader ecological networks, including relationships with mutualists and commensals, and non-target species, to better understand community-level consequences.

Addressing these challenges will require interdisciplinary approaches, combining laboratory experiments, field studies, molecular identification, and ecological modeling to bridge mechanistic insights with practical applications. By tackling these priorities, the next decade of research can deepen our understanding of arthropod–fungal interactions and translate this knowledge into strategies that support both ecosystem resilience and sustainable management of arthropod pests.

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