Chapter 9

Towards integrating interaction networks into global parasite conservation: insights from bats, bat flies and their fungal associates

Jonathan Cazabonne[1,2,3,*], Danny Haelewaters[4,5,6,*], Aimée Blondelle[4,7], Melissa Ingala de Waal[8]

[1]Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada
[2]Chaire UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada
[3]Centre d'Étude de la Forêt, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada
[4]Research Group Mycology, Department of Biology, Ghent University, 9000 Ghent, Belgium
[5]Biology Centre of the Czech Academy of Sciences, Institute of Entomology, 370 05 České Budějovice, Czechia
[6]Department of Zoology, Faculty of Science, University of South Bohemia, 370 05 České Budějovice, Czechia
[7]Meise Botanic Garden, 1860 Meise, Belgium
[8]Department of Biological Sciences, Fairleigh Dickinson University, Madison, NJ 07940, USA

*Corresponding authors - Jonathan Cazabonne, cazabonne.jonathan@gmail.com; Danny Haelewaters, danny.haelewaters@gmail.com

Abstract

Parasites are a key conservation blind spot. Even though parasitism is a widespread ecological lifestyle, most parasite diversity remains unknown, as do the interactions in which they are involved. Some parasite species are involved in multitrophic interactions, meaning they span multiple trophic levels. These complex interactions are generally understudied, and conservation frameworks fail to integrate them. The interaction network involving bats, bat flies, and bat fly-associated fungal parasites of the order Laboulbeniales provides a case study for identifying knowledge and conservation gaps in multitrophic interaction systems. In this chapter, we review the role of parasites and species interactions in conservation frameworks, as well as our current understanding of this tripartite parasitic and hyperparasitic system. We discuss gaps in species diversity and distribution (Linnean and Wallacean shortfalls), responses to abiotic environments (Hutchinsonian shortfall), ecological interactions across and within trophic levels (Eltonian shortfall), and the cascading consequences of host extinction on other partners in the interaction (Scarian and Ostromian shortfalls). We also discuss how species interactions, especially obligate ones, could be integrated into conservation schemes such as Red Listing, and we propose a simple conceptual framework to support this. Finally, we present outstanding questions and future directions, with the hope that they will foster collaborations and research in the field of multitrophic interactions, and contribute to a better understanding and protection of complex interaction networks in the face of global change.

Keywords: Arthropod-associated fungi, cross-kingdom interactions, fungal conservation, IUCN Red List, knowledge shortfalls

1. The place of parasites in biological conservation

Biodiversity conservation strategies have always had blind spots. This is most evident in taxonomic coverage, with certain groups of organisms (e.g., charismatic animals and plants) receiving more protection than others (e.g., microorganisms). However, there are also biases regarding the lifestyle that conservation efforts focus on. Parasites are a particularly clear example of this. Although they are increasingly recognized as representing a highly diverse pool of species and having important regulatory effects on ecosystems (Hudson *et al*., 2006), parasites remain understudied, are rarely incorporated in biodiversity conservation planning, and continue to be associated with strong prejudices. Indeed, both the scientific community and the general public have long regarded parasites from a human, animal, or plant health perspective in which they should not be protected (Windsor, 1997). This observation can be linked to the way wildlife management tends to divide biodiversity into two categories: threats to biodiversity on the one hand, and targets for conservation on the other (Dougherty *et al*., 2015). Despite the challenges faced by parasites in being recognized as components of biodiversity with their own intrinsic right to be protected, many scientists have, for several decades, called for a paradigm shift to integrate parasites into conservation biology.

More than thirty years ago, Donald A. Windsor highlighted that parasites were largely absent from conservation biology, which traditionally focused instead on free-living animals and plants (Windsor, 1995). He also emphasized that while efforts were made to protect individual species, the full complement of parasites associated with those hosts was overlooked. Twenty-five years later, an international working group of parasitologists and ecologists proposed twelve goals to be achieved by 2030, aimed at identifying and filling knowledge and conservation gaps for parasites (Carlson *et al*., 2020). These goals cover areas such as data collection and synthesis, risk assessment and prioritization, conservation practices, as well as outreach and education. As is the case for other organisms, identifying gaps in parasite conservation is a prerequisite for being able to address and fill them. Beyond their intrinsic value, parasites deserve protection because (i) they are extremely diverse and ubiquitous in natural ecosystems; (ii) they in likelihood outnumber free-living organisms, providing models to study ecological interactions and the evolution of inter-species relationships; (iii) they play numerous ecological and evolutionary roles, such as regulating natural populations and driving host evolution; and (iv) they are often threatened, with many species potentially already extinct (Gómez and Nichols, 2013; Lymbery and Smit, 2023). These points challenge the common misconception that parasitism is only harmful, showing that parasites also play important positive roles in ecosystems—and, ultimately, for humans (Szopieray and Żbikowska, 2021). Given that parasites are interconnected with the rest of life, often via highly dependent, obligate interactions, they have even been proposed as promising conservation tools, notably by using parasites as indicators of the impacts of global change drivers on their hosts (Gagne *et al*., 2022).

All these efforts are gradually bearing fruit in terms of parasite conservation. For example, in 2023, a Parasite Specialist Group was established under the Species Survival Commission of the International Union for Conservation of Nature (IUCN) (Hopkins and Kwak, 2023) with three main goals: (1) to carry out assessments of parasitic metazoan species (excluding human and domesticated animal parasites), (2) advance conservation efforts for threatened parasites, and (3) increase awareness about parasite conservation (https://www.iucnparasites.com/). Several important projects and milestones have already emerged from this group, including recovery plans for the Ryukyu rabbit tick (*Haemaphysalis pentalagi*, Arthropoda: Ixodidae) on the Amami rabbit (*Pentalagus furnessi*, Mammalia: Leporidae) on Amami Island in the Ryukyu Islands of southern Japan, and the Manx shearwater flea (*Ceratophyllus fionnus*, Arthropoda: Ceratophyllidae) on the Manx shearwater (*Puffinus puffinus*, Aves: Procellariidae) on the Isle of Rùm off the coast of Scotland, as well as the objective of completing 50 IUCN Red List assessments of parasites (Hopkins and Kwak, 2024). Conferences and workshops are also being organized. To cite a few, for example, a thematic session at the 2024 IUCN Regional Conservation Forum for Europe, North, and Central Asia in Bruges (Belgium), a Parasite Conservation symposium at the 2025 International Congress for Conservation Biology in Brisbane (Australia), as well as Red Listing workshops at Hasselt University (Belgium) in 2024 and at the 2025 Annual Meeting of the American Society of Parasitologists in Winston-Salem, North Carolina (USA).

Other initiatives have also emerged in recent years in favor of parasite conservation outreach and science communication. For example, the Global Parasitologist Coalition (https://www.globalpc.org/) develops education material to foster engagement of scientists and the public with parasites and their conservation (Li *et al*., 2025). The World Archives of Species Perception (WASP), an initiative that aims to study public perception of global biodiversity in a systematic way (Nguyen *et al.* 2023), now includes a project on parasites (http://www.wasp-project.net/wasp-p). Lastly, citizen science is increasingly being leveraged to help document interactions between hosts and their (often unknown) parasites. The Terrestrial Parasite Tracker (TPT) has launched a project, Notes from Nature (https://www.zooniverse.org/projects/md68135/notes-from-nature-terrestrial-parasite-tracker/about/research), that allows people to help digitize collections of arthropod parasites and their terrestrial vertebrate hosts. Despite these advances, challenges and gaps remain regarding the perspective of parasites being fully mainstream in conservation frameworks and in people's vision of biodiversity.

Parasites remain vastly underrepresented in the IUCN Red List. In 2015, only one animal parasite species was listed, the pygmy hog-sucking louse (*Haematopinus oliveri*, Arthropoda: Haematopinidae), which was classified as critically endangered along with its host, the pygmy hog (*Porcula salvania*, Mammalia: Suidae) (Rocha *et al*., 2016). Even with the objective of 50 parasite species being assessed by the IUCN SSC Parasite Specialist Group, this would represent less than 0.001% of all species assessed to date (i.e., of the 172,620 species in IUCN Red List version 2025-02; UICN, 2026). Parasites are also sensitive to global change and face extinction risks. Taking the example of parasitic worms, Carlson *et al.* (2017) predicted up to 30% may be prone to extinction due to changing climate, accounting for co-extinction with hosts. Recently, Boast *et al.* (2025) observed a decline in parasite richness following the population decline of the endangered kākāpō parrot (*Strigops habroptilus*, Aves: Strigopidae), and a continued loss of parasites even after the host population rebounded. This suggests that parasite extinctions may be far more widespread and significant than previously assumed.

Parasites are also routinely overlooked in international biodiversity laws such that parasite conservation does not reflect current parasitology research on their diversity, threats, and extinction risks (Claerhoudt, 2024). This situation mirrors the fact that parasitology research is still underfunded and underrepresented in conservation research compared to vertebrates (Di Marco *et al*., 2017; Mammola *et al*., 2020). Moreover, studies that explicitly consider parasites as targets for conservation remain less numerous compared to those framing parasites primarily as threats. Lymbery and Lymbery (2024) recently looked at this issue by analyzing articles published in the *International Journal for Parasitology*, *Biological Conservation*, and *Conservation Biology*. One takeaway from their study is that Windsor's (1995) call for 'equal rights for parasites' is still far from being realized. Finally, scientists are also pointing out new gaps that need attention to build a more transdisciplinary approach to parasite conservation—one that could lead to stronger conservation outcomes. These include, for example, sociocultural factors and the philosophical foundations of why and how parasites should be conserved (Brown *et al*., 2025). Recently, in a call to turn current knowledge into action for parasite conservation, Hopkins and Wood (2026) argued that (1) some parasite species already have sufficient data available to be assessed for the IUCN Red List, (2) the current IUCN framework is already adequate and that more effort should be directed toward actually assessing parasite species, (3) considering hosts alongside their parasites would support a co-conservation approach that, when possible, protects both interacting partners, and (4) there is a need to build a community of practice willing to collect data, provide expertise, and carry out IUCN assessments.

2. From conservation of individuals to species interactions

Historically, the pragmatic approach to conservation focused on individual species. This strategy was adopted as a quick and efficient way to guide spatial prioritization efforts, with the assumption that protecting a target species would indirectly benefit many others (Runge *et al*., 2019). Examples of conservation efforts that focus on individual species include flagship, umbrella, and keystone species. Flagship species are usually charismatic organisms that capture public attention, evoke emotions or sympathy, and generally attract more funding for conservation efforts (Thomas-Walters and Raihani, 2017). Umbrella species are those whose protection is expected to provide indirect benefits to a broader suite of species that co-occur within the same habitat (Roberge and Angelstam, 2004; Branton and Richardson, 2011). Finally, keystone species are generally defined as having a disproportionately large ecological impact relative to their abundance in the ecosystem (Power *et al*., 1996). However, some environmental laws that focused on protecting a handful of such key species were developed before conservation biology fully recognized the importance of species interactions in shaping natural population dynamics and ecosystems, and that the loss of "strongly interactive species" (sensu Soulé *et al*., 2005) can lead to negative consequences for the whole ecosystem. Conservation biology has therefore gradually shifted from a species-centered perspective to one that integrates species interactions—at the same time as we came to realize that many ecosystem functions actually emerge from complex networks of interactions among species

(Heleno *et al*., 2012). Nowadays, many conservationists call for interaction and ecological networks to be effectively integrated in conservation frameworks, with, for example, discussions around which network-level structural indicators deserve attention from a conservation perspective (e.g., Tylianakis *et al*., 2010; Heleno *et al*., 2012; Dansereau *et al*., 2025).

In addition to the transition from species-focused to species interaction conservation, conservation biology has also undergone a shift in how it views the very nature of interactions. The historical view of interactions are bi-trophic, such as plant–herbivore or predator–prey interactions (Riley, 1892; Tyson *et al.*, 2010). However, researchers have shown that many bi-trophic interactions actually do not occur in isolation but are interconnected through cascading effects—which has been quite extensively demonstrated, for example, for plant-herbivore-parasitoid or pathogens systems (e.g., Eber, 2001; Meiners, 2015). Another example of this shift in perspective is the plant–soil system, which for a long time was studied separately but was later brought together, particularly with the rise of studies on plant–mycorrhizal fungi interactions in agricultural and forest contexts. However, research has shown that mycorrhizal fungi can also exert a variety of direct or indirect influences on plant-associated aboveground herbivores and foliar endophytic communities, as well as soil-borne pathogens (Tscharntke and Hawkins, 2002; Bennett *et al*., 2006; Razak and Gange, 2023).

All these interactions can be of various types, but a flourishing area of research in the field of multitrophic interactions has been parasitic interactions. Indeed, parasites teach us that interactions are not just host-parasite, one-to-one relationships, but also networks and multitrophic (Furlong and Pell, 2005). Parasites are increasingly recognized as key components of interaction networks and food webs. Because of their wide range of interactions—ranging from generalist to highly host-specific, and often spanning one or multiple hosts—they are thought to increase both the complexity and the connectivity of ecological networks and food webs (Lafferty *et al*., 2006, 2008; Hatcher *et al*., 2012). Looking at host–parasite interactions—whether bipartite or multitrophic—through the lens of networks has helped us better understand their ecological and evolutionary dynamics, move from description to prediction, and explore how environmental factors shape these interactions through space and time (Poulin, 2010; Runghen *et al*., 2021).

Another research area that has reshaped our understanding of host–parasite interactions is hyperparasitism, where parasites themselves can be parasitized by other, secondary parasites. This type of interaction is particularly noteworthy because it is obligate—meaning the hyperparasite can only survive by parasitizing a primary parasite that itself depends on an infected host. Obligate hyperparasitism is thought to have evolved from facultative parasitism as an opportunistic pathway to specialize on primary parasites as a directly available source of food (Sullivan, 2009). Hyperparasitism has also been quite extensively studied in the plant–aphid–primary parasitoid–hyperparasitoid model systems, mainly due to the fact that aphids are economically important as crop pests, and they are easy to rear in laboratory (e.g., Sullivan and Völkl, 1999; Sullivan, 2009). Beyond adding another level of trophic interaction, hyperparasitism also has important implications for biological control, for example in contexts where the hyperparasite has a positive or negative effect on species that are beneficial or harmful for controlling invasive species or crop pests (Sullivan, 2009). It is worth noting here that parasitism itself can have applications for biological control. An interesting recent example is the ongoing research on the potential of using *Hesperomyces harmoniae* from the understudied order Laboulbeniales (class Laboulbeniomycetes) as biocontrol agent against the invasive harlequin ladybird, *Harmonia axyridis* (Arthropoda: Coccinellidae) (Haelewaters *et al*., 2017c; Xie *et al*., 2026). That said, knowing that many parasites are arthropods or interact with arthropods, and that over 1 million insect species have been described while 80% remain to be discovered (see Stork, 2018), this highlights the vast extent of multitrophic interactions involving arthropods that are still unknown and to be understood.

One of the most diverse but also understudied interactions in multitrophic research and conservation is between arthropods and fungi. Interaction between fungi and arthropods are widespread and common in natural populations, whether they are mutualistic or parasitic (Roy *et al*., 2006; Blackwell and Vega, 2018). In terms of species diversity, with an estimated 2.5 million of fungal species (Niskanen et al. 2023), fungi represent the second-most diverse group of organisms after arthropods. Insects represent one of the still largely unexplored habitats for fungi, where a substantial portion of still unknown diversity of fungal parasites and pathogens is predicted to be found (see Hawksworth and Rossman, 1997; Vega and Blackwell, 2005; Araújo and Hughes, 2016; Blackwell and Vega, 2018). Moreover, arthropods and fungi have an evolutionary history of relationships dating back more than 300 millions years and serve as models for understanding the ecology and evolution of cross-kingdom host–parasite systems, such as their spatial distribution patterns and coevolution processes (Haelewaters *et al*., 2021).

Although we know that many fungal species are involved in multitrophic interactions with arthropods and animals more broadly, our understanding of the diversity of these systems, the influence of the environment on these networks, and the nature of interactions across trophic levels remains very limited. These knowledge gaps—particularly pronounced in neglected groups of fungal parasites—hinder further efforts to integrate such complex interaction networks into conservation frameworks. A striking example of these knowledge and conservation gaps is that the IUCN Red List does not currently take species interactions into account in its assessment processes. Using multitrophic interaction models could help such an endeavor.

3. Interactions across trophic levels: the example of the bat–bat fly–fungus system

As biodiversity adapts to an increasingly complex world, conservation actions must take into account multi-scale interactions among species of conservation concerns and their parasites, along with the broader environment and all other interacting species (Speer *et al*., 2020). Yet, under the current conceptual framework in conservation biology, it remains difficult to clearly identify causal relationships across different levels of trophic interactions that could be used to guide conservation and management priorities. Hyperparasitism is an especially interesting model in this regard because, by influencing a parasite species, a hyperparasite can indirectly affect the primary host in multiple ways, and therefore, the whole environment (Gleason *et al*., 2014). In particular, the obligate multitrophic interaction linking bats (Mammalia: Chiroptera), bat flies (Diptera: Hippoboscoidea), and fungal ectoparasites (Laboulbeniomycetes: Laboulbeniales) is receiving growing attention and has been proposed as a model system to help fill the knowledge and conservation gaps mentioned above (**Fig. 1**).

Even though hyperparasitism is assumed to be fairly common, only a handful of obligate host–parasite–hyperparasite systems have been well studied to date and used as model systems to address broader questions in community ecology and network theory (Haelewaters *et al*., 2021). The arguments supporting the case for using the system involving bats, their blood-sucking ectoparasitic flies, and fly-associated fungal ectoparasites as a valuable obligate multitrophic interaction model system are multifold:

1. This system is widespread globally and can be studied almost anywhere around the globe.
2. Gaining more insights into the diversity patterns of bats and their parasites will inevitably transcend research fields, as bats and bat flies are frequently studied for their zoonotic potential (Goldberg *et al*., 2017; Abundes-Gallegos *et al*., 2018; Xu *et al*., 2019; Lee *et al*., 2021; Ramírez-Martínez *et al*., 2021; Chomel *et al*., 2023).
3. Bats have important ecosystem functions, including pest control and pollination, and are estimated to be worth $3.7 billion/year in North American agriculture alone (Boyles *et al*., 2011).
4. From an eco-evolutionary perspective, bats and their parasites represent an opportunity to study biogeographical patterns across trophic levels, because each host bat acts as a naturally replicated, standardized “microhabitat” for their respective parasite communities (Tello *et al*., 2008; Torchin *et al*., 2015; Ingala de Waal *et al*., 2025). When regarding bats as microhabitats, their different body parts provide local habitat heterogeneity (Hiller *et al*., 2018), which in turn sustain parasite communities competing for resources and partitioning niches.
5. This multitrophic network is extremely specialized (i.e., with high host specificity across trophic levels; de Groot *et al*., 2020), increasing its vulnerability to co-extinction (Colwell *et al*., 2012; Ozman-Sullivan and Sullivan, 2023) due to the delicate balance between host and parasite (Koh *et al*., 2004). This opens up the potential of studying extinction cascades within this system. This is especially relevant given that bats are heavily threatened globally, with 221 species listed in one of the threatened categories in the IUCN Red List (Frick *et al*., 2020; IUCN, 2026).
6. Parasitic fungi and their host insects form a great opportunity to study co-evolutionary processes due to their short generation times (Joop and Vilcinskas, 2016).
7. There is great potential to integrate other organisms interacting with each trophic level of the system (e.g., bat- and bat fly-associated viruses, bacteria and microparasites, Szentiványi *et al*. 2019, Speer *et al*., 2020; or bacterial biofilms associated with Laboulbeniales thalli, Lubbers *et al*., 2022), thereby allowing for a broader network-based approach to study multitrophic interactions across kingdoms.
8. Despite the growing recent interest in this system, it remains overlooked and has been studied only descriptively, with many gaps persisting—such as in understanding its diversity and distribution (Linnean and Wallacean shortfalls), its responses to environmental change (Hutchinsonian shortfall), the interactions both among species and across trophic levels (Eltonian shortfall), and the cascading consequences of host extinction on the other partners in the interaction (Scottian and Ostromian shortfalls).

9. Finally, each partner in this interaction is considered non-charismatic (see Boso *et al.*, 2021; Cazabonne *et al.*, 2025), resulting in this multitrophic system being either unpopular or largely unknown to the general public, and not considered in conservation efforts. Further research on this system has the potential to spark greater public engagement with the conservation of non-charismatic species—traditionally sidelined in conservation policies—as well as with the protection of their interactions.

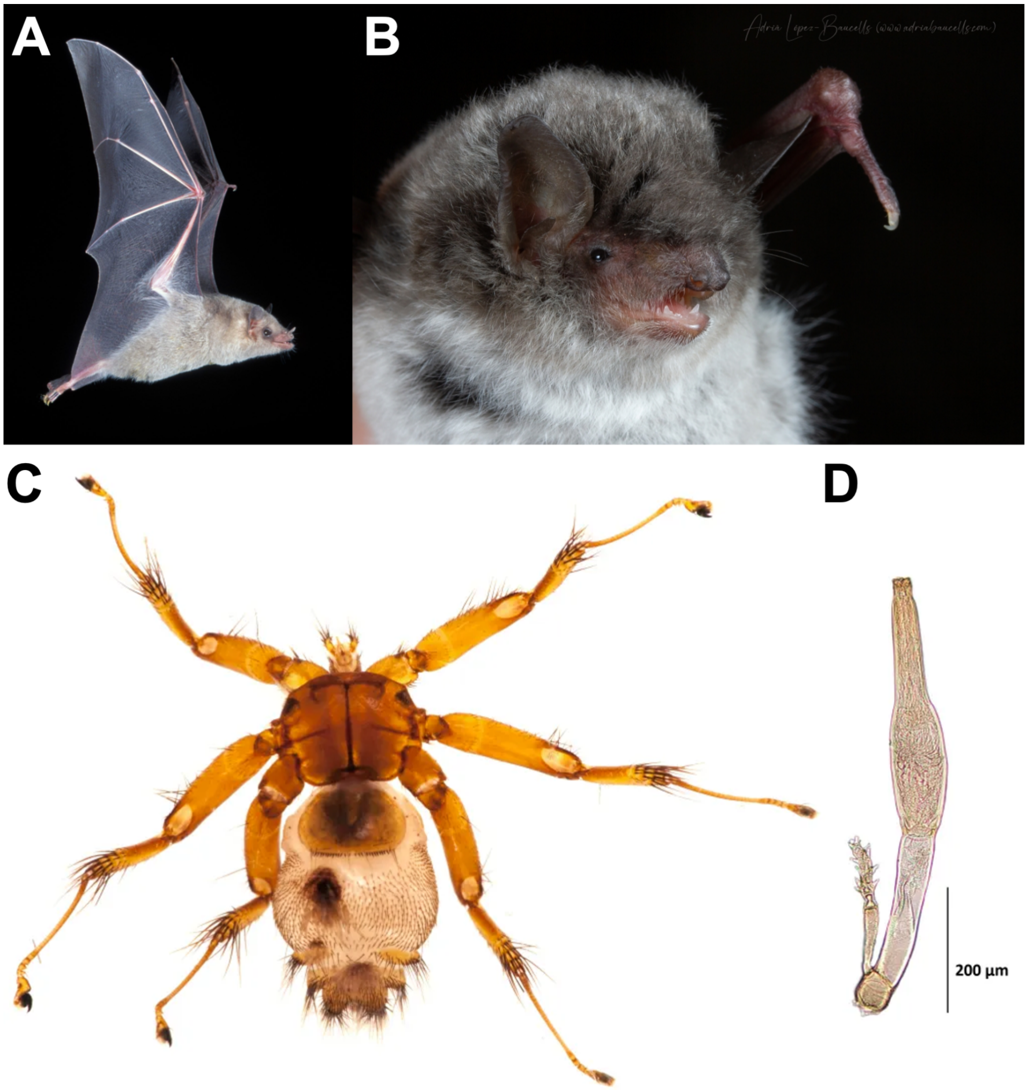

Figure 1. Selected photographs of bats, bat flies, and hyperparasitic Laboulbeniales. **A**. *Leptonycteris nivalis* (IUCN Endangered). **B**. *Myotis capaccinii* (IUCN Vulnerable). **C**. *Penicillidia conspicua*. **D**. *Arthrorhynchus nycteribiae.* Credits: **A**. J. Scott Altenbach, **B**. Adrià López-Baucells, **C**, **D**. Danny Haelewaters.

3.1. Species diversity

Bats (Mammalia: Chiroptera), serving as the primary host in these associations, are the second-most successful group of mammals in terms of species diversity, with around 1500 species currently recognized (Simmons and Cirranello, 2025). Present on nearly every continent, they play an essential role in ecosystems as insectivores, pollinators and seed dispersers (Ramírez-Fráncel *et al*., 2022). Bats are host to a wide range of parasite species, including several ecto- and haemoparasites (Marshall, 1982; Szentiványi *et al*., 2019).

A striking group among these parasites are bat flies (Diptera: Hippoboscoidea), highly derived arthropods that feed off the bat's blood and have co-evolved alongside bats since the Eocene (Dittmar *et al*., 2015). As obligate ectoparasites, they exhibit a high degree of host specificity, and they are only able to survive for a limited time off-host (Overal, 1980; Dick, 2007; Dick and Dittmar, 2014). These parasitic dipterans are viviparous, only leaving their host for pupa deposit (Dittmar *et al*., 2009). Currently, two families are recognized: Nycteribiidae and Streblidae (Dick and Dittmar, 2014). Each family is roughly restricted to a hemisphere: Nycteribiidae are predominantly found on Eastern Hemisphere bats (Europe, Africa, Asia, Oceania), whereas Streblidae are most speciose in the tropics of the Western Hemisphere (North and South America) (Dick and Patterson, 2006). While Nycteribiidae are recognizable by their striking resemblance to arachnids, Streblidae are less confined to one particular habitus, exhibiting diverse morphologies ranging from winged to wingless, laterally compressed or dorsoventrally flattened (Dick and Patterson, 2006). Nycteribiidae currently counts 285 species in 11 genera globally (Graciolli and Dick, 2018). For Streblidae, recent checklists report 252 species in 35 genera (Dick and Graciolli, 2018).

Some of these bat flies can be host to parasites themselves, thus partaking in hyperparasitic associations. One such instance are Laboulbeniales (Ascomycota: Laboulbeniomycetes), which are an order of microscopic ectoparasitic fungi (Haelewaters *et al*., 2019, 2021a). Laboulbeniales have radiated widely across the spectrum of hosts and can be found on representatives from the subphyla Chelicerata, Hexapoda, and Myriapoda (Haelewaters *et al*., 2021a). Currently over 2400 species have been described in 145 genera, and many are thought to be undiscovered, with estimates of the true diversity pointing towards 75,000 species (Weir and Hammond, 1997; Haelewaters *et al*., 2021a, 2022a; Kaishian, 2021). Laboulbeniales fungi are characterized by a peculiar morphology. When released from the perithecium, sticky, two-celled ascospores will adhere to the host integument (Blackwell *et al*., 2020). Spore transmission has been demonstrated to mainly rely on direct contact between hosts, e.g., through grooming or mating. Once they are out in the open, spores have limited survival capacities, limiting the opportunities for transfer through the environment (De Kesel, 1995). Upon attachment to the new host (or the same host in case of auto-infection), consecutive mitotic divisions will lead to the formation of a multicellular receptacle, an antheridia-bearing appendage and one or multiple perithecia.

Four genera are known to associate with bat flies: *Arthrorhynchus*, *Dimeromyces*, *Gloeandromyces*, and *Nycteromyces*. The genus *Gloeandromyces* is currently the most speciose, with 10 species (Haelewaters *et al*., 2017b; Haelewaters and Pfister, 2019; Liu *et al*., 2020; Van Caenegem *et al*., 2023). In *Arthrorhynchus*, six species are recognized, but this number is debated due to hypothesized synonymy on the one hand and cryptic diversity on the other (Haelewaters *et al*., 2017a, 2020). In *Nycteromyces*, only two species are presently known, and also *Dimeromyces* encompasses two bat fly-associated species in addition to many other that are associated with different host groups (Dogonniuck *et al*., 2019).

Another instance of secondary parasitism associated with bats are neotromboid mites that live on streblid bat flies. Only one species of mite (*Monunguis streblida* (Trombidiformes: Neotrombidiidae) has been described for this association. For this species, only larval stadia are known, and the adults remain uncollected (Lindquist and Vercammen, 1971). This hyperparasitic interaction has only been reported for Brazil, Colombia, Mexico, and the West Indies, on seven species of bat flies (da Silva Reis *et al*., 2019; López-Rivera *et al*., 2024).

For some Laboulbeniales species, biofilms consisting of bacterial colonies have been found on the thallus surfaces (Lubbers *et al*., 2022). These have not been brought into culture yet. As a result, the identity of the bacteria populating these biofilms remains unknown. These bacterial communities could produce antimicrobial compounds or contribute to the development of ascospores to mature thalli, but this remains speculative.

Bat flies have also been suggested to play a role in the transmission of *Pseudogymnoascus destructans* or *Pd* (Ascomycota: Leotiomycetes), the causal agent of white-nose syndrome, which has had a devastating effect on North-American bat populations (Hoyt *et al*., 2021). The possibility of bat ectoparasites as vectors for this ascomycete was explored for *Spinturnix* mites by Lučan *et al*. (2016), where all wing mite samples tested positive for *P. destructans* DNA. Zahradníková *et al*. (2018) additionally detected *P. destructans* DNA on bat flies, further supportive of this theory. Another study found species-specific alterations in the skin microbiome of bats infected with white-nose syndrome. For one species, skin microbiome diversity was found to be remarkably lower, whereas in other species included in this study, diversity remained unaltered regardless of *P. destructans* presence (Ange-Stark *et al*., 2023).

The study of bat-associated parasites and hyperparasites has been hampered by knowledge gaps in current diversity assessments. In Laboulbeniomycetes, the Linnean shortfall is expected to be very high, as many species are yet to be described (Haelewaters *et al*., 2024a). For Laboulbeniales associated with bat flies, research has been especially limited. The reasons for this are multifold. First of all, infection prevalences of bat flies with Laboulbeniales are low to very low, ranging from 3 to 7% in the Eastern and Western Hemisphere respectively (Blackwell, 1980; Haelewaters *et al*., 2017a; Haelewaters *et al*., 2021b). This implies that many bat fly specimens need to be screened in order to detect infected individuals. An added hurdle is the presence of both cryptic diversity as well as morphological plasticity in these bat fly-associated Laboulbeniales, which makes the inclusion of molecular data into species descriptions indispensable (Haelewaters and Pfister, 2019; Haelewaters *et al*., 2020; Van Caenegem *et al*., 2023, 2026).

3.2. Response to the abiotic environment

Another important aspect of the conservation of fungal parasites is understanding how both the parasites and the interacting partners respond to abiotic environmental changes (Hutchinsonian shortfall), especially anthropogenic-driven ones (Wolinska and King, 2009) (**Fig. 2**). Although data remain very scarce on how this multitrophic system responds to abiotic factors (Haelewaters *et al*., 2018a, 2018b), some studies suggest that abiotic factors such as climate change and habitat modification do affect the partners across trophic levels.

Bats are organisms known to be sensitive to climate change and anthropogenic-induced disturbances, with lasting efforts to detect current and predict future impacts of these changes on multiple aspects of their diversity, ecology, distribution, and reproduction (e.g., Duchamp and Swihart, 2008; Adams, 2010; Sherwin *et al*., 2012; García-Morales *et al*., 2013; Korine *et al*., 2016; Hayes and Adams, 2017; Festa *et al*., 2023; Van de Vuurst *et al*., 2025). For example, Dondini *et al*. (2025) showed in a long-term monitoring study in Italy that bat population size is modulated by fluctuations in precipitation and that bat phenology is modified by climate change, possibly impacting reproductive success. Hussain *et al*. (2025) showed that for the Indian flying fox (*Pteropus medius*, Chiroptera: Pteropodidae), temperature and humidity are among the most important factors determining roost site selection and populations are negatively affected by tree cutting and hunting. However, the response of bat flies to environmental changes has been comparatively less studied. Pilosof *et al*. (2012) showed that human population density and climate change-related factors (i.e., temperature, precipitation, elevation) had indirect negative influence on the abundance of bat flies across four American tropical bat species in Venezuela. Bats and their interaction with bat flies have also been found to be directly and indirectly influenced by forest loss, habitat fragmentation, and landscape modification (Meyer *et al*., 2016; Hiller *et al*., 2020; Palheta *et al*., 2020; Eriksson *et al*., 2023). Bats and their bat flies are also known to be sensible to climate change-related factors. For example, studies have suggested that climatic seasonal variations and microclimate could affect bat fly species composition, their prevalence, and intensity (e.g., Patrício *et al*., 2016; Zarazúa-Carbajal *et al*., 2016; Salinas-Ramos *et al*., 2018; Barbier *et al*., 2021; Tlapaya-Romero *et al*., 2021), but these responses may be species-dependent.

For bat fly-associated fungal ectoparasites, this type of knowledge is even more limited. Szentiványi *et al*. (2019) studied the effects of climate change factors on the fungal parasites associated with ants (*Myrmica scabrinodis*) and bat flies (*Nycteribia schmidlii* and *Penicillidia conspicua*), and showed that Laboulbeniales parasites were more likely to be present under low annual mean temperature and humidity. These results should be treated with some caution, given limited sampling, non-standardized collecting methods, and use of outside climatic data (instead of data from within bat roosts/ant nests, which likely have greater importance). Péter *et al*. (2022) hypothesized that higher humidity levels may enhance the spread of bat fly-associated Laboulbeniales infections. More recently, Burazerović *et al*. (2025a) reported that the presence and prevalence of *A. nycteribiae* on *P. conspicua* were significantly influenced by seasons. The authors attributed these patterns primarily to seasonal variations in bat fly density, which would influence the chances of transmission from one host to another and therefore fungal reproductive success. They also observed differences in the prevalence of *A. nycteribiae* on *P. conspicua* between eastern and western Serbia, but the extent to which these differences can be explained by variations in abiotic environmental factors across geographical scales remains to be further investigated. To our knowledge, studies looking at the effects of abiotic environmental variables on Laboulbeniales parasitism in controlled laboratory experiments have been conducted only for *Hesperomyces harmoniae* associated with an invasive ladybird (see Haelewaters *et al*., 2022; de Groot *et al*., 2025). How abiotic factors, whether they are linked or not to anthropogenic disturbances, affect the presence and prevalence of Laboulbeniales on bat flies remain largely unknown to date. Monitoring both outside abiotic variables and/or microclimatic variables in roost environments (see Péter *et al*., 2022) will be important avenues to help answer these questions.

Several limitations hinder our ability to fully resolve the Hutchinsonian shortfall for the bat–bat fly–fungus multitrophic system. First, most of the studies exploring the response of this system to abiotic environmental changes have focused on a single species or trophic level, not at the community-level. However, as it has been suspected for other trophic systems like plant–insect interactions (e.g., de Sassi *et al*., 2012; Zhu *et al*., 2015), the responses of bats, bat flies, and fungal parasites to environmental changes are likely to be modulated at the community scale, both within and across trophic levels (Pedersen and Fenton, 2007; Tylianakis *et al*., 2008; Walther, 2010; Rynkiewicz *et al*., 2015). It therefore remains unknown what the direct effects of environmental changes are on each trophic level, as well as the indirect cascade effects mediated through interspecific interactions—e.g., how climate change-driven effects on bats may indirectly influence bat flies and their fungal parasites, and vice versa.

Second, current literature on the effects of environmental changes on this system, especially on the parasites, is geographically limited. For example, most studies exploring the effects of logging and habitat modification on bat flies have been conducted in the American tropics, whereas studies focusing on the links between Laboulbeniales parasites and environmental variables are mainly from Central Europe. In future studies, more geographically-spread localities should be included, notably in regions where the landscape matrix mixes natural and managed habitats and where the effects of climate change are expected to be important.

Third, the response of parasites in this system is mostly assessed through the lens of prevalence, intensity, and species diversity, which are classically used measures in parasitology (e.g., Rózsa *et al*., 2000). Beyond that, it would be interesting for future studies to also explore the effects of environmental changes on these parasites using a broader range of response variables, e.g., related to parasite morphology, phenology, ecology, and interaction network metrics. Identifying different types of traits in bats, bat fly parasites, and their hyperparasites, and examining how these traits vary in response to abiotic factors, will help build a trait-based approach to understanding how these multitrophic interactions respond to environmental changes (Marjakangas *et al*., 2022; de Bello *et al*., 2025).

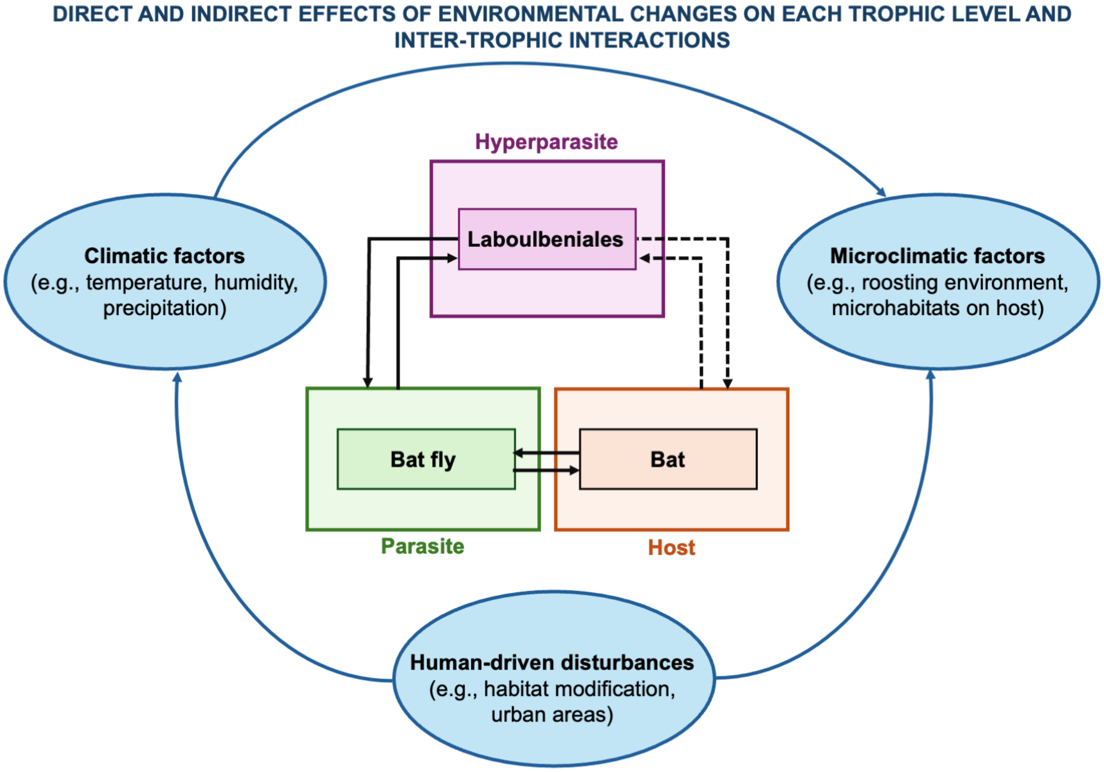

Figure 2. Schematic illustration of direct and indirect effects of abiotic traits on each trophic level and on interactions between trophic levels. For simplicity, only the principal direct and indirect effects are shown. Solid arrows indicate direct interactions, while dashed arrows represent indirect interactions.

3.3. Ecological interaction across trophic levels

The partners of an interaction system are not isolated units, but instead mediators of complex interactions within and between each trophic level. Indeed, multiples levels of interactions can occur: (i) direct and indirect (or latent) interactions across trophic levels, i.e., interactions between bats and bat flies, between bat flies and their fungal parasites (**Tab. 1**), and also between bats and the bat fly-associated fungal parasites; and (ii) intra- or inter-species interaction within trophic levels (Ingala de Waal *et al*., 2025). Furthermore, each partner of this system has an associated microbiome (Speer *et al*., 2022), and interactions among these microbiomes across and within trophic levels may also occur (i.e., holobiont–holobiont interactions; Skičková *et al*., 2025), although they remain largely understudied (**Fig. 3**).

Bat fly sex appears to be an important factor affecting Laboulbeniales infection prevalence, with infections more commonly observed in females than in males. This is likely due to the fact that females live longer, are physically larger, and have more fat reserves than males (Haelewaters *et al*., 2017a; Szentiványi *et al*., 2018; Péter *et al*., 2022; Burazerović *et al*., 2025a). The relationship of bat fly ecomorphology with parasitism was explored by de Groot et al. (2020); they suggested that, at the species-level, the presence of hyperparasites may be associated with positions on bat flies that are linked to their ecomorphological type, such as the long hind legs of fur-runners. Such position specificity has already been observed in Laboulbeniales infecting other hosts (e.g., Goldmann and Weir, 2012), but the lack of quantitative data on this multitrophic system prevents similar investigations for bat fly-associated hyperparasites. Indeed, Hiller *et al*. (2018) quantitatively demonstrated that hind leg morphology determines bat fly ecomorphological groups. That would suggest the morphological characteristics associated with bat fly ecological type should be considered when assessing Laboulbeniales position specificity patterns in future studies. An interesting hypothesis that could be further explored is whether distinct ecomorphological groups can be defined for the hyperparasite, and whether these ecomorphotypes are explained by their position of growth on the host integument. Factors driving morphological differences within phylogenetic species of bat fly-associated Laboulbenialesare are still unknown to date (Haelewaters *et al*., 2018). Haelewaters and Pfister (2019) showed the existence of position-induced morphological plasticity and multiple morphotypes depending on the position on the host within phylogenetic species. Dogonniuck *et al*. (2019) also suggested that intra-specific variations may result from growing on different positions of the host integument. Laboulbeniales morphotypes (e.g., *Gloeandromyces plesiosaurus* f. *asymmetricus* and f. *plesiosaurus*; Van Caenegem *et al*., 2023) are probably the result of morphological adaptations induced by position-related stresses (e.g., nutrient availability). However, as with the effects of abiotic factors on this multitrophic system, the lack of comprehensive, standardized datasets spanning multiple trophic levels currently prevents us from assessing and answering these types of questions.

Beyond the influence of bat flies on Laboulbeniales parasitism, the hyperparasite may in turn have an impact on its host. However, this type of knowledge for bat-associated Laboulbeniales is also still very limited (de Groot *et al*., 2020). In-situ or in-lab studies exploring the effects of Laboulbeniales parasitism on their hosts have mainly focused on two study systems, namely *Rickia wasmannii* on *Myrmica* ants (e.g., Csata *et al*., 2014; Báthori *et al*., 2015, 2017) and *He. harmoniae* on *Harmonia axyridis* ladybirds (e.g., Haelewaters *et al*., 2020). A few studies have also explored the effects of *Stigmatomyces majewskii* on *Drosophila suzukii* (Yamazaki *et al*., 2023). To our knowledge, only one published study studied the effects of Laboulbeniales parasitism on bat flies using *A. eucampsipodae* and *A. nycteribiae* infecting *Nycteribia schmidlii* and *Penicillidia conspicua* bat flies (Szentiványi *et al*., 2020). The authors showed that survival rates of *P. conspicua* were reduced by half as a result of infection by Laboulbeniales, whereas no significant effects of fungal infection were observed for *N. schmidlii*. These results suggest that the effects of hyperparasitism on bat fly parasites may depend on bat fly species, and likely also on the Laboulbeniales species involved. Beyond impacting bat fly life span, Laboulbeniales hyperparasitism could likely also influence population size, density, and individual reproductive success of bat flies (Szentiványi and Estók, 2024). However, further studies covering a broader range of bat fly and Laboulbeniales species are needed to explore these questions more in depth. Moreover, the mechanisms underlying these negative effects on bat fly hosts remain largely unknown, but they are likely related to the lifestyle of the hyperparasites. Indeed, light microscopy, transmission electron microscopy and three-dimensional reconstructions based on micro-computed tomography have confirmed that *A. nycteribiae* possesses a haustorium that attaches to the bat fly host and presumably serves to acquire nutrients (Reboleira *et al*., 2021).

However, studies directly investigating nutrient and matter transfer between hyperparasites and bat flies are still needed to confirm these mechanisms.

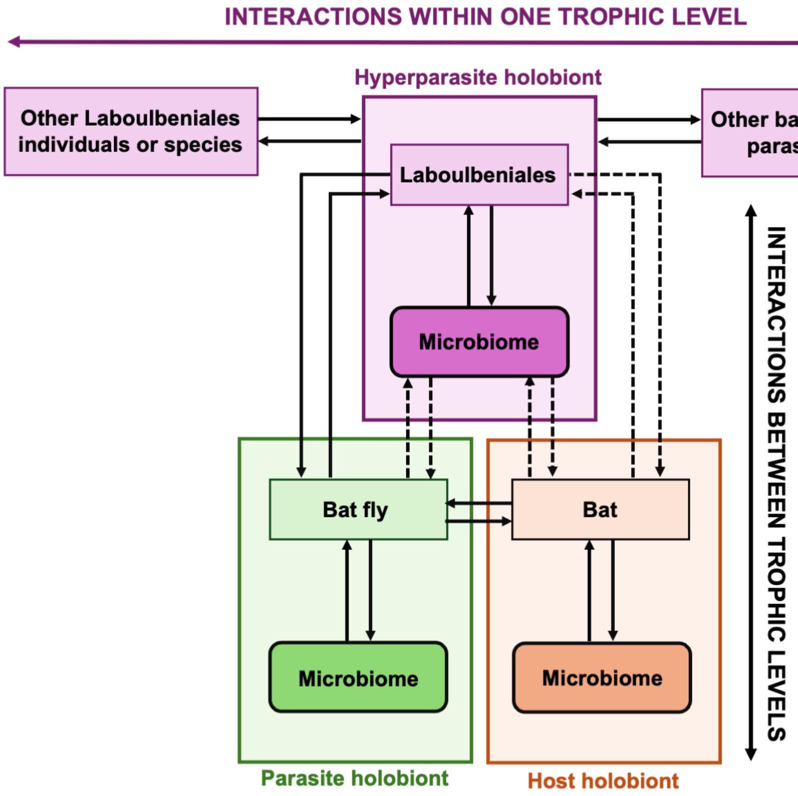

Figure 3. Schematic illustration of the interactions occurring between and across trophic levels in the bat–bat fly–fungus multitrophic system. Solid arrows indicate direct interactions, while dashed arrows indicate indirect interactions. To avoid overcrowding the figure, within-trophic interactions are illustrated using only the example of the hyperparasite.

Indirect interactions may also occur between bats and the hyperparasite of their ectoparasite. For example, Péter *et al*. (2022) showed that bat host behavior, social behavior, and roost selection may influence parasitism of Laboulbeniales on their bat flies using data from southeastern Europe. They found that Laboulbeniales more likely infect bat flies found on bat females and bats that roost together in close proximity and in underground environments like caves. Burazerović *et al*. (2025a) also found slightly higher infections by Laboulbeniales on bat flies found on bat females, likely due to the fact that females form denser and larger groups during pregnancy and when raising young individuals. These cascading effects across multiple trophic levels are often more difficult to detect because they are indirect, but they are important to consider in order to obtain a full understanding of the ecological interactions that shape multitrophic interaction networks and, ultimately, how they shape species- and community-level responses to environmental changes.

Table 1. Summary of Laboulbeniales species associated with bat flies.

Genus	**species**	**Bat fly hosts**	**Source(s)**
Arthrorhynchus	*acrandros*	*Phthiridium biarticulatum*	Merola (1952)
Arthrorhynchus	*cyclopodiae*	*Cyclopodia macrura*	Thaxter (1901)
Arthrorhynchus	*diesingii*	*Nycteribia vexata*	Kolenati (1857)
Arthrorhynchus	*diesingii* [as A. eucampsipodae]	*Nycteribia schmidlii*	Haelewaters *et al*., (2017a)
Arthrorhynchus	cf. *diesingii* [as *A. eucampsipodae*]	*Nycteribia kolenatii*	Blackwell (1980)
Arthrorhynchus	cf. *diesingii* [as *A. eucampsipodae*]	*Nycteribia pedicularia*	Blackwell (1980)
Arthrorhynchus	*eucampsipodae*	*Eucampsipoda hyrtlii*	Thaxter (1901)
Arthrorhynchus	*eucampsipodae*	*Eucampsipoda africana*	Haelewaters *et al*., (2020)
Arthrorhynchus	*eucampsipodae* sensu lato	*Basilia pumila*	Blackwell (1980)
Arthrorhynchus	*eucampsipodae* sensu lato	*Nycteribia progressa [as Eremoctenia progressa]*	Balazuc (1971)
Arthrorhynchus	*eucampsipodae* sensu lato	*Nycteribia schmidlii scotti*	Blackwell (1980)
Arthrorhynchus	*eucampsipodae* sensu lato	*Cyclopodia ferrarii*	Blackwell (1980)
Arthrorhynchus	*eucampsipodae* sensu lato	*Nycteribia parvula*	Blackwell (1980)
Arthrorhynchus	*eucampsipodae* sensu lato	*Eucampsipoda inermis*	Blackwell (1980)
Arthrorhynchus	*nycteribiae*	*Penicillidia conspicua*	Haelewaters *et al*., (2017b).
Arthrorhynchus	*nycteribiae*	*Penicillidia dufourii*	Haelewaters *et al*., (2017b).
Arthrorhynchus	*nycteribiae* sensu lato	*Phthiridium biarticulatum*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Penicillidia fulvida*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Penicillidia pachymela*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Penicillidia oceanica oceanica*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Penicillidia indica*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Penicillidia jenynsii*	Thaxter (1931)
Arthrorhynchus	*nycteribiae* sensu lato	*Phthiridium ceylonicum*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Phthiridium phillipsi*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Nycteribia pedicularia*	Ryberg (1947)
Arthrorhynchus	*nycteribiae* sensu lato	*Nycteribia latreillii*	Balazuc (1971)
Arthrorhynchus	*nycteribiae* sensu lato	*Nycteribia schmidlii*	Blackwell (1980)
Arthrorhynchus	*nycteribiae* sensu lato	*Nycteribia blasii*	Balazuc (1971)
Arthrorhynchus	*nycteribiae* sensu lato	*Nycteribia kolenatii*	Nosawad (1973)
Arthrorhynchus	*nycteribiae* sensu lato	*Eucampsipoda africana*	Haelewaters *et al*., (2020)
Arthrorhynchus	*westrumbii*	*Penicillidia conspicua*	Kolenati (1857)
Dimeromyces	*capensis*	*Brachytarsina africana*	Dogonniuck *et al*., (2019)

Dimeromyces	*streblidarum*	*Brachytarsina amboinensis*	Dogonniuck *et al*., (2019)
Gloeandromyces	*cusucoensis*	*Trichobius uniformis*	Van Caenegem *et al*., (2023)
Gloeandromyces	*dickii*	*Trichobius joblingi*	Haelewaters & Pfister (2019)
Gloeandromyces	*diversiformis* f. *diversiformis*	*Strebla wiedemanni*	Van Caenegem *et al*., (2023)
Gloeandromyces	*diversiformis* f. *musiformis*	*Strebla wiedemanni*	Van Caenegem *et al*., (2023)
Gloeandromyces	*diversiformis* f. *vanillicarpiformis*	*Strebla wiedemanni*	Van Caenegem *et al*., (2023)
Gloeandromyces	*hilleri*	*Mastoptera guimaraesi*	Liu *et al*., (2020)
Gloeandromyces	*nycteribiidarum*	*Megistopoda aranea*	Thaxter (1931)
Gloeandromyces	*nycteribiidarum* sensu lato	*Trichobius yunkeri*	Haelewaters *et al*., (2017b)
Gloeandromyces	*nycteribiidarum* sensu lato	*Exastinion clovisi*	Van Caenegem *et al*., (2023)
Gloeandromyces	*nycteribiidarum* sensu lato	*Trichobius sparsus*	Van Caenegem *et al*., (2023)
Gloeandromyces	*pageanus* f. *pageanus*	*Trichobius dugesioides*	Haelewaters & Pfister (2019)
Gloeandromyces	*pageanus* f. *alarum*	*Trichobius joblingi*	Haelewaters & Pfister (2019)
Gloeandromyces	*pageanus* f. *polymorphus*	*Trichobius dugesioides*	Haelewaters & Pfister (2019)
Gloeandromyces	*pageanus* f. *polymorphus*	*Trichobius joblingi*	Haelewaters & Pfister (2019)
Gloeandromyces	*plesiosaurus* f. *plesiosaurus*	*Trichobius yunkeri*	Van Caenegem *et al*., (2023)
Gloeandromyces	*plesiosaurus* f. *asymmetricus*	*Trichobius yunkeri*	Van Caenegem *et al*., (2023)
Gloeandromyces	*pseudodickii*	*Trichobius longipes*	Van Caenegem *et al*., (2023)
Gloeandromyces	*streblae* f. *streblae*	*Strebla wiedemanni*	Thaxter (1931)
Gloeandromyces	*streblae* f. *streblae*	*Trichobius joblingi*	Haelewaters & Pfister (2019)
Gloeandromyces	*streblae* f. *streblae*	*Trichobius dugesioides*	Haelewaters & Pfister (2019)
Gloeandromyces	*streblae* f. *sigmomorphus*	*Trichobius joblingi*	Haelewaters & Pfister (2019)
Gloeandromyces	*verbekeniae* f. *verbekeniae*	*Strebla galindoi*	Van Caenegem *et al*., (2023)
Gloeandromyces	*verbekeniae* f. *inflexus*	*Strebla galindoi*	Van Caenegem *et al*., (2023)
Nycteromyces	*orientalis*	*Brachytarsina alluaudi*	Dogonniuck *et al*., (2019)

Nycteromyces	*orientalis*	*Brachytarsina africana*	Dogonniuck *et al*., (2019)
Nycteromyces	*orientalis*	*Brachytarsina amboinensis*	Dogonniuck *et al*., (2019)
Nycteromyces	*orientalis*	*Brachytarsina modesta*	Dogonniuck *et al*., (2019)
Nycteromyces	*streblidinus*	*Strebla wiedemanni*	Thaxter (1917)

3.4. Conservation of interactions

The growing importance of multitrophic interactions and interaction networks in the literature also highlights how current conservation actions and metrics still largely fail to take these phenomena into account. Currently, the IUCN Red List is based on the assessments of single species and does not allow to consider the dimension of interacting species. Similarly, other conservation avenues, such as protected areas, Key Biodiversity Areas (KBAs), Alliance for Zero Extinction (AZE) and Evolutionarily Distinct and Globally Endangered (EDGE) species approaches, are also built on single-species assessments, as are most national and continental biodiversity protection laws. This is particularly concerning given that co-extinctions and cascading extinction events are one of the least understood threats to biodiversity, especially when it comes to parasite diversity and ecological functions (Dunn *et al.,* 2009; Lafferty, 2012; Strona, 2015; Okamura *et al*., 2018; Herrera *et al*., 2021; Truter *et al*., 2025). Many parasites in host–parasite systems still remain undescribed and could potentially go extinct before being described (e.g., Brian and Aldridge, 2022).

In the case of bats, they face many threats and represent a major conservation concern, particularly due to their high sensitivity to habitat fragmentation and disease (Mickleburgh *et al*., 2002; Frick *et al*., 2020). Based on the dataset compiled by de Groot *et al*. (2020), to date, among the bat species associated with Laboulbeniales-bearing bat flies, one species is considered Endangered (*Leptonycteris nivalis*) and two are classified as Vulnerable (*Myotis capaccinii* and *Miniopterus schreibersii*) on the IUCN Red List (**Fig. 4**). Only *Gloeandromyces nycteribiidarum* has been recorded in association with an Endangered bat host, while three Laboulbeniales species (*Arthrorhynchus eucampsipodae*, *A. nycteribiae*, *Nycteromyces orientalis*) have been found associated with at least one bat host listed as Vulnerable (**Fig. 4**). Interestingly, the fact that Laboulbeniales species identified to species or even genus are associated with bat hosts listed as Vulnerable or Near Threatened highlights that still-undescribed Laboulbeniales diversity may already be facing extinction risks, especially considering that there are 24 Critically Endangered, 88 Endangered, and 109 Vulnerable bat species overall (IUCN, 2026). One could argue that in such a system of obligate interactions across trophic levels, if bat hosts are considered threatened, then the Laboulbeniales species associated with bat flies found on those hosts—and the bat flies themselves—should be given at least similar conservation attention, as they are likely exposed to comparable threats and extinction risks. It is nevertheless likely that many Laboulbeniales and bat fly species associated with already threatened bat hosts likely face similar threats and potentially comparable extinction risks, especially those species that display high host specificity.

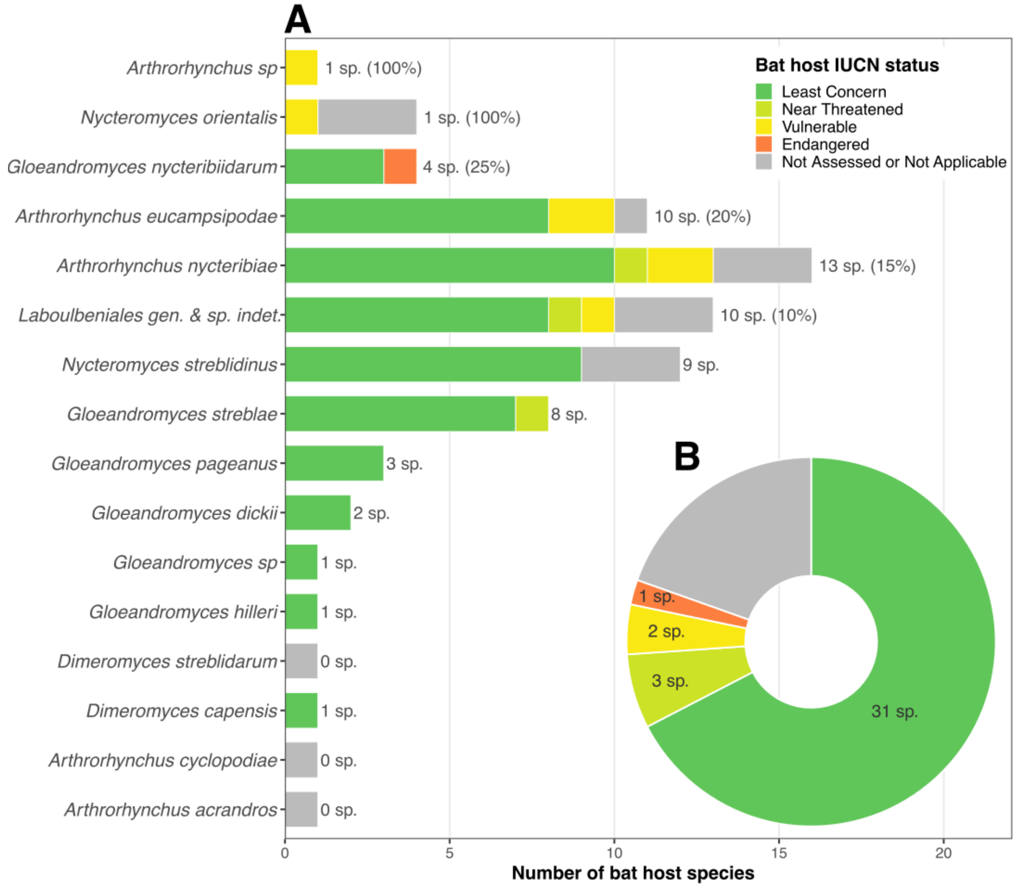

Figure 4. IUCN Red List status of bat species associated with bat flies known to host Laboulbeniales. **A.** For each Laboulbeniales species recorded in association with bat flies found on bat hosts, IUCN conservation status of the corresponding bat species is indicated. Note that "*Laboulbeniales gen.* & *sp. indet.*" represents multiple undescribed and/or unidentified genera and species. To the right of each bar, the total number of bat species with known IUCN status is shown, and in parentheses, when applicable, the percentage of those species classified as threatened (Vulnerable or Endangered; no Critically Endangered bat species were present in the analyzed dataset). **B.** Pie chart showing the proportion of IUCN statuses among bat species according to the IUCN Red List (v. 2025–2). Bat host species that could not be identified to species level or that have not been evaluated are grouped under the category “Not Assessed or Not Applicable”. Data compiled and edited from de Groot et al. (2020).

The conservation of species interactions comes with many challenges that limit their integration into conservation frameworks. For example, questions remain about which metrics or traits of interaction networks should be preserved to maintain network stability and functioning in a conservation perspective (Tylianakis *et al.*, 2010). As discussed in previous sections, the many knowledge gaps regarding species diversity, geographic distribution, interactions with other species, and responses to environmental change all represent data shortfalls that make it difficult for conservation frameworks to shift from species-focused to interaction network-focused approach goals. There is therefore a need to develop ecological frameworks that account for species interactions and cascading effects across trophic levels in order to better understand these complex interaction networks and to encourage the integration of fungal parasites into conservation goals (de Groot *et al*., 2020; Ingala de Waal *et al*., 2025). Beyond advocating for the conservation of species interactions and helping prevent cascading extinctions, such ecological frameworks could also help better understand, protect and manage parasite diversity and the ecological functions and ecosystem services supported by these interaction networks (see Heinen *et al*., 2020; Lymbery and Smit, 2023; Haelewaters *et al*., 2026b).

5. Solutions to fill knowledge and conservation shortfalls of complex interaction networks

5.1. Long-term multitrophic sampling and databases

Knowledge of this tripartite and hyperparasitic interaction system is biased toward bats, with virtually nothing known about the Laboulbeniales ectoparasites infecting bat flies. Studying this system requires sampling the bat host, then searching for bat flies, and finally screening those flies for the presence of Laboulbeniales infections. Such a sampling scheme is meticulous and time-consuming, and often requires the screening of hundreds to thousands of bat flies to collect a few thalli given the generally low prevalence of these ectoparasites on their hosts. Therefore, researchers working on this system have called for the development of unbiased, large-scale datasets spanning all three trophic levels in order to help fill knowledge and conservation shortfalls (Haelewaters *et al*., 2018, 2021b). Achieving this requires increased bat sampling across a range of ecosystem types, but this also raises questions about which monitoring approaches should be implemented. Haelewaters *et al*. (2024b) recently showed that standardized approaches do not perform equally well across different habitats and are not a “one-size-fits-all” solution, suggesting that bat sampling techniques need to be adapted to the specific ecosystem being surveyed.

Such multitrophic sampling efforts and databases also need to be global in scope. Most regions worldwide have not been specifically surveyed to study this multitrophic interaction system, which means that our current understanding remains strongly geographically biased. Increasing sampling efforts for bats, bat flies, and their parasitic fungi—especially in understudied regions and habitats, but also in areas that have already been surveyed—often leads to new country records, new host–parasite associations and the discovery of undescribed Laboulbeniales species. For example, López-Rivera *et al*. (2024), while sampling for hyperparasites of bat flies in Colombia, recently reported a likely undescribed species of *Gloeandromyces* parasitizing *Paratrichobius longicrus* (Streblidae) bat flies. To address these gaps, comprehensive sampling efforts spanning bats, bat flies, and their fungal parasites should be encouraged across a wide range of ecosystems, habitat types, and sites globally. Moreover, it is known that a way to minimize bias and obtain the most comprehensive picture of fungal diversity at a given site is through repeated, long-term monitoring (Stallman *et al*., 2024). Sampling approaches should therefore include repeated monitoring of bats at selected sites over several years.

5.2. Working with other disciplines

Collaborations across actors, disciplines, and countries is key to achieving conservation goals (Kark *et al*., 2015). A prominent example is the growing involvement of citizen scientists and non-professionals in data collection for conservation purposes across many fields of research, including mycology (Irga *et al*., 2018; Haelewaters *et al*., 2024a, 2026a). Another historical example are the benefits that collaborations between mammalogists and parasitologists can bring in expanding diversity and ecological research (Galbreath *et al*., 2019). Similarly, since mammalogists, parasitologists, and mycologists working on this interaction system all capture bats for their respective research, this synergy could be taken advantage of to foster cross-disciplinary collaborations, help increase sampling efforts and advance conservation for all species involved in these interactions (Haelewaters *et al*., 2021b). In this case, mammalogists can greatly help broaden the scope of research conducted by those studying parasites and hyperparasites by sampling bat flies while capturing bats and making these specimens available for screening for hyperparasites by mycologists. Since the field of fungal conservation is relatively young compared to that of animals and plants, such cross-disciplinary collaborations across countries will play an important role for the development of this research area and to ensure that its impact reaches beyond the mycological community—because other organismal groups can only benefit if all fungi are better protected (Minter, 2011). We therefore believe that mammalogists and parasitologists working with bat flies are in a good position to help draw attention to this parasitic and hyperparasitic tripartite interaction system and to the need to better understand and protect it.

5.3. Leveraging new approaches and conceptual frameworks

5.3.1 Integrative taxonomy

Studying the diversity of understudied, cryptic groups or interaction systems comes with many challenges, one of the foremost being how to delimit species. The approach now widely adopted to describe fungal species is integrative taxonomy, which involves combining as many independent lines of evidence as possible for species delimitation, such as morphology, geometric morphometrics, molecular phylogenetics, sequence-based identification, ecology and information on habitats, and geography (Lücking *et al*., 2021; Stengel *et al*., 2022). Integrative taxonomy has already shown its usefulness to describe diversity across a wide range of fungal groups, especially in those with many cryptic species (Maharachchikumbura *et al*., 2021; Ekanayaka *et al*., 2025). Integrative taxonomy approaches are becoming increasingly standard, but there is still much work to be done for researchers working with bat flies and Laboulbeniales (Haelewaters *et al*., 2021b). Even though bats are the second-largest group of mammals in terms of species number (Findley, 1995), there are still species unknown to science, especially in understudied areas and habitats (e.g., Novaes *et al*., 2021; Curran *et al*., 2022; Barquez *et al*., 2023; Grunwald *et al*., 2023; Wang *et al*., 2024; Saikia *et al*., 2025). This is the same situation for bat flies and Laboulbeniaes, which both are poorly studied groups, with new species recently described and many more awaiting formal descriptions (e.g., for bat flies: Ramasindrazana *et al*., 2017; Hrycyna *et al*., 2022; Tlapaya-Romero *et al*., 2023; for Laboulbeniales: Dogonniuck *et al*., 2019; Liu *et al*., 2020; Van Caenegem *et al*., 2023). Using integrative taxonomy to identify new species of parasitic bat flies and hyperparasitic Laboulbeniales, combined with large-scale multitrophic sampling and databases, will help close the Linnean shortfall and open up new research opportunities in this system, like unraveling patterns of diversity and host specificity across trophic levels and geographic regions (e.g., latitudinal diversity gradients, see e.g., Weir, 2004; Haelewaters *et al*., 2021c).

5.3.2 Omics tools

Another growing approach is the use of omics technologies to study the diversity, ecology and interactions between species (Xu, 2006; Cuadros-Orellana *et al*., 2013). The use of environmental DNA metabarcoding could help improve our understanding of the microorganism communities associated with each of the species involved in these multitrophic interactions. This approach could, for example, be applied to detect emerging fungal diseases in bat hosts, such as white-nose syndrome caused by *Pd* (e.g., Wang *et al*., 2026), as well as other pathogens (Dhivahar *et al*., 2023). It could also help characterize microbial communities associated with bat flies and Laboulbeniales thalli (e.g., Lubbers *et al*., 2022; André *et al*., 2023; Marcatti *et al*., 2025). When combined with genome sequencing and annotation, and metatranscriptomic approaches, these tools could also shed light on the mechanisms underlying interactions among and within the three trophic levels (e.g., Moreno Santillan *et al*., 2021; Porter *et al*., 2022; Koga *et al*., 2024; Huang *et al*., 2025). Since genome-based studies in Laboulbeniomycetes are still in their infancy, only one draft genome of a Laboulbeniomycete species has been published to date, i.e., *Herpomyces periplanetae* (Haelewaters *et al*., 2020), but ongoing efforts are underway to sequence representative species across the Laboulbeniomycetes tree, including species associated with bat flies (Cazabonne *et al*., 2025). These tools open the door to a range of new exciting research questions, for example, whether and how pathogens move from one trophic level to another, what consequences this has for each trophic level, and how bat flies or Laboulbeniales respond to the presence of other parasites or organisms sharing the same host. Answering these questions will help develop a more holistic and integrated understanding of the diversity and functioning of multitrophic interaction networks as a whole.

5.3.3 Bring parasites and hyperparasites into conservation

Haelewaters *et al*. (2024a) recently described the Scottian shortfall, which quantifies the lack of IUCN Red List assessments in a given group of organisms. For bats, this shortfall is relatively small, as the vast majority of bat species have been evaluated. Out of the roughly 1,500 known bat species (Simmons and Cirranello, 2025), 89% (i.e., 1,336 species) have been assessed against IUCN criteria (IUCN, 2026). To date, no species of bat flies or Laboulbeniales ectoparasites have been assessed for the IUCN Red List. This hinders the integration of these poorly studied groups into conservation plans or actions that are based on assessed species. With global, unbiased sampling and datasets for this multitrophic system, data could be gathered on the distribution, population trends of these species and the threats they face, and lead to the very first IUCN Red List assessments for these groups. As noted by Hopkins and Wood (2026), the current IUCN Red List framework and criteria are already sufficient to assess parasitic species when enough data are available, and it is the increasing participation of parasitologists in data collection and IUCN assessments that will be key to advancing parasite conservation.

We also advocate for the integration of known species interactions and their existing conservation status (if any) into the IUCN assessment process rather than making species assessments individually. Indeed, for example, a species listed as Least Concern could be pushed to extinction if its host disappears or is considered threatened (i.e., co-extinction events). If a host goes extinct, its uniquely associated parasites will inevitably vanish too, along with their hyperparasites. We term this series of hidden and indirect, trickle-down effects across multiple trophic levels “dark cascades”. These dark cascades may also lead to what has been termed “dark extinctions” (see Boehm and Cronk, 2021, Essl *et al*., 2026), meaning in our case the extinction of parasites and hyperparasites that have not yet been described. Considering host–parasite and multitrophic interactions involving parasites in IUCN Red Listing will help implement conservation actions that are both parasite-safe and host-safe, and help manage potential conflicts that may arise between the conservation of the parasite and its host (Hopkins and Wood, 2026).

To contribute to the discussion on how organisms involved in obligate multitrophic interactions could be protected, we propose a simple conceptual framework based on the existing IUCNRed List for integrating obligate species interactions into IUCN species assessments (**Fig. 5**). Since this research domain remains largely unexplored, we encourage the scientific community working on this multitrophic interaction system, as well as on species involved in obligate interactions more broadly, to conduct IUCN assessments that explicitly consider species interactions. We also encourage the mycological and parasitological research communities to consider developing guidelines to facilitate the interpretation of IUCN criteria for obligate interactions (e.g., generation lengths between host and parasite, definition of individuals, etc.). There is also a need to develop and propose a solid, globally applicable conceptual framework to study extinction cascades and to build models that assess and predict potential biodiversity collapses of parasites following host extinctions.

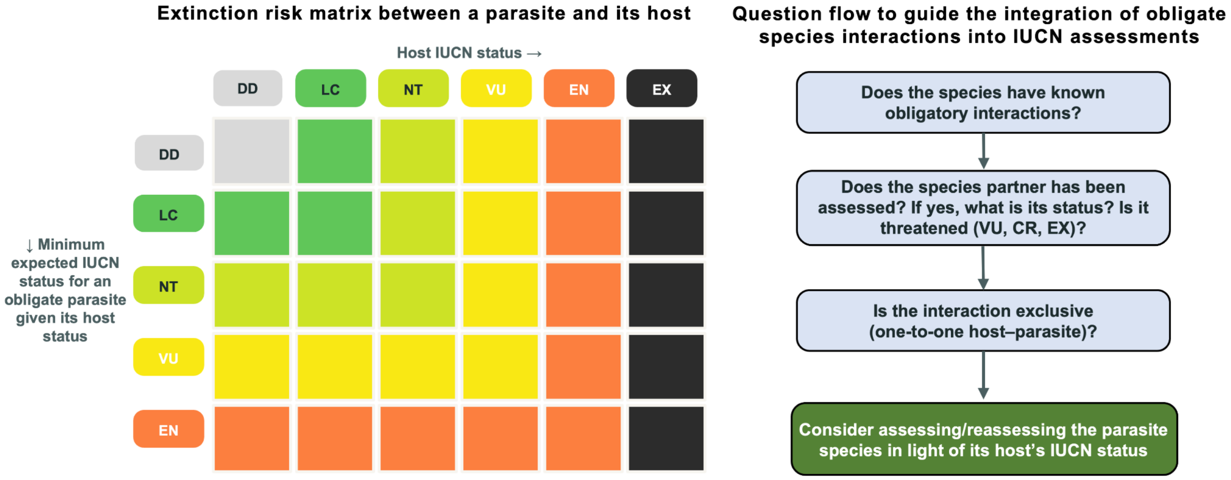

Figure 5. Conceptual framework for integrating obligate species interactions into IUCN assessments. On the left, a conceptual matrix illustrating the minimum extinction risk expected for an obligate parasite based on the IUCN status of its host. For a given parasite status, the more threatened the host is, the greater the extinction risk for the obligate parasite. On the right, a series of three simple questions that can be asked during the assessment or reassessment of a parasite species to ensure that its assigned status is considered in light of the IUCN status of its host.

6. Implications for other host-parasite multitrophic interaction networks

This chapter focuses on the tripartite bat–bat fly–fungus study system, but the knowledge and conservation gaps identified here, as well as the solutions proposed to address them, could also apply to other host–parasite multitrophic interaction networks that are in need of study. For example, another interesting multitrophic interaction involving Laboulbeniales is the one with species of *Trenomyces*, which parasitize lice that themselves parasitize birds, such as woodpeckers and domestic chickens (e.g., Chatton and Picard, 1909; Thaxter, 1926). While the bat–bat fly–fungus system has recently received increasing attention in the literature, these hyperparasites and their interactions with arthropod parasites of other mammals remain comparatively understudied. Given that nearly all organisms on the planet are involved in at least one parasitic relationship, the number of potential obligate multitrophic interactions is likely very high. Other types of multitrophic interactions, more or less obligate, are also gaining attention—for example, interactions between fungal pathogens, insect hosts, and their associated bacteria (e.g., Płoszka *et al*., 2025), or between endophytes, host plants, and soil mycorrhizal fungi (e.g., Afkhami *et al*., 2020). We believe that the framework and approaches proposed in this chapter could also benefit the study and conservation of these other multitrophic interaction systems.

7. Future directions: a synergistic, system-based ecological framework to better know and protect complex interaction network

Even though parasitism is one of the most widespread lifestyles in the living world, parasites continue to suffer from a bad reputation and remain among the least studied and least protected organisms. Multitrophic interactions involving parasites offer new opportunities to better understand diversity across trophic levels, how biotic and abiotic factors influence interactions both between and within trophic levels, how these interactions respond to anthropogenic disturbances and current or future global changes, and how we can better protect species interactions within conservation frameworks. Based on the remaining knowledge gaps, the challenges we face, and potential solutions to advance the study and conservation of parasites in the light of the bat–bat fly–fungus system, we outline a list of future directions and research priorities in the field of multitrophic interactions involving fungal parasites.

1. Describe the taxonomic and phylogenetic diversity across trophic levels and how it is geographically distributed using integrative taxonomy approaches. Sampling efforts should cover different types of ecosystems and regions of the world, ideally targeting understudied habitats.
2. Understand how abiotic factors influence interactions across trophic levels. In particular: how environmental changes linked to local microclimatic conditions and bat roosting habits, or human-driven disturbances affect Laboulbeniales parasitism on bat flies.
3. Understand species interactions both across and within trophic levels. In particular, what is the influence of other parasites or pathogens on Laboulbeniales parasitism of bat flies? Does infection of bats with pathogens affect Laboulbeniales parasitism on their bat flies?

4. Develop long-term, global, unbiased, and trait-based sampling schemes and databases to study the diversity, ecology, and conservation of multitrophic interactions.
5. Build bridges between disciplines and foster collaborations with other conservationists working with mammals and arthropods to leverage sampling synergies, raise awareness, and advance parasite conservation beyond disciplinary and national boundaries.
6. Integrate species interactions into conservation frameworks, particularly IUCN Red Listing. Conduct IUCN assessments for all species involved in multitrophic interactions, taking into account the IUCN status and threats faced by hosts when assessing or reassessing parasite species.
7. Create a global, cross-country, and cross-discipline ecological framework that considers interacting species as a whole to better understand and protect multitrophic interactions.

To address these questions and close knowledge and conservation shortfalls in this field, new tools and approaches should be leveraged, such as integrative taxonomy, omics techniques, conservation metrics and tools, as well as novel statistical and modeling approaches. We hope that the example of the bat–bat fly–Laboulbeniales system can serve as a model to deepen our understanding of multitrophic interactions involving fungal parasites, while also providing insights applicable to other types of multitrophic interactions, whether or not they involve fungi. We also hope that increasing research in these fields will help ensure that species interactions across trophic levels are one day taken into account in ecosystem management and conservation strategies across multiple temporal and spatial scales.

Acknowledgements

We would like to thank Thomas E. Martin (Operation Wallacea) and Warre Van Caenegem (Biology Centre of the Czech Academy of Sciences) for providing insightful edits and comments on an earlier version of this manuscript. J. Cazabonne acknowledges support from the Fonds de Recherche du Québec - Nature et technologies through a B2X doctoral research fellowship (https://doi.org/10.69777/347942, no. 347942). D. Haelewaters is supported by the Czech Academy of Sciences (Lumina Quaeruntur Fellowship LQ200962501). A. Blondelle is supported by the Research Foundation Flanders (Meise–FWO PhD Fundamental Research Fellowship 1157426N).

References

Abundes-Gallegos, J., Salas-Rojas, M., Galvez-Romero, G., Perea-Martínez, L., Obregón-Morales, C.Y., Morales-Malacara, J.B., et al, 2018. Detection of dengue virus in bat flies (Diptera: Streblidae) of common vampire bats, *Desmodus rotundus*, in Progreso, Hidalgo, Mexico. Vector-Borne and Zoonotic Diseases 18 (1), 70–73.

Adams, R.A., 2010. Bat reproduction declines when conditions mimic climate change projections for western North America. Ecology 91 (8), 2437–2445.

Afkhami, M.E., Almeida, B.K., Hernandez, D.J., Kiesewetter, K.N., Revillini, D.P., 2020. Tripartite mutualisms as models for understanding plant–microbial interactions. Current opinion in plant biology 56, 28–36.

Ange-Stark, M., Parise, K.L., Cheng, T.L., Hoyt, J.R., Langwig, K.E., Frick, W.F., et al., 2023. White-nose syndrome restructures bat skin microbiomes. Microbiology Spectrum 11 (6), e02715–23.

Araújo, J.P., Hughes, D.P., 2016. Diversity of entomopathogenic fungi: which groups conquered the insect body? Advances in Genetics 94, 1–39.

Balazuc, J., 1971. Notes sur les Laboulbéniales. III. Rectifications, synonymies et mises au point (suite). Bulletin mensuel de la Société linnéenne de Lyon 40, 211–216.

Barbier, E., Falcão, F., Bernard, E., 2021. Bat-ectoparasitic fly relationships in a seasonally dry tropical forest in Brazil. Parasitology Research, 120 (10), 3507–3517.

Barquez, R.M., Tomasco, I.H., Sánchez, R.T., Boero, L., Rodriguez, A.D., Díaz, M.M., 2023. A new species of bat in the genus Nyctinomops Miller, 1902 (Chiroptera: Molossidae) from Misiones, Argentina. Journal of Mammalogy 104 (5), 1062–1071.

Bennett, A.E., Alers-Garcia, J., Bever, J.D., 2006. Three-way interactions among mutualistic mycorrhizal fungi, plants, and plant enemies: hypotheses and synthesis. American Naturalist 167 (2), 141–152.

Blackwell, M., 1980. Incidence, host specificity, distribution, and morphological variation in *Arthrorhynchus nycteribiae* and *A. eucampsipodae* (Laboulbeniomycetes). Mycologia 72 (1), 143–158.

Blackwell, M., Vega, F.E., 2018. Lives within lives: Hidden fungal biodiversity and the importance of conservation. Fungal Ecology 35, 127–134.

Boast, A.P., Wood, J.R., Bolstridge, N., Perry, G.L., Wilmshurst, J.M., 2025. Long-term parasite decline associated with near extinction and conservation of the critically endangered kākāpō parrot. Current Biology 35 (16), 3920–3929.

Boehm, M., Cronk, Q.C., 2021. Dark extinction: the problem of unknown historical extinctions. Biology Letters 17 (3), 20210007.

Boso, A., Álvarez, B., Pérez, B., Imio, J.C., Altamirano, A., Lisón, F., 2021. Understanding human attitudes towards bats and the role of information and aesthetics to boost a positive response as a conservation tool. Animal Conservation, 24 (6), 937–945.

Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. Science 332 (6025), 41–42.

Branton, M., Richardson, J.S., 2011. Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. Conservation Biology 25 (1), 9–20.

Brian, J.I., & Aldridge, D.C., 2022. Mussel parasite richness and risk of extinction. Conservation Biology 36 (6), e13979.

Brown, T.M., Dunn, A.M., Quinnell, R.J., Clarke, E., Cunningham, A.A., Goodman, S.J., 2025. An interdisciplinary approach to improving conservation outcomes for parasites. Conservation Biology 39 (1), e14431.

Burazerović, J., Arsenijević, S., Jovanović, M., Obradović, M., Tomanović, S., 2025a. Seasonal patterns and host traits as drivers of ectoparasite abundance in three bat species (*Miniopterus schreibersii*, *Rhinolophus euryale* and *Rhinolophus ferrumequinum*) in the Central Balkans. Current Zoology (accepted). https://doi.org/10.1093/cz/zoaf079

Burazerović, J., Jovanović, M., Savković, Ž., Breka, K., Stupar, M., 2025b. Finding the right host in the darkness of the cave—new insights into the ecology and spatio-temporal dynamics of hyperparasitic fungi (*Arthrorhynchus nycteribiae*, Laboulbeniales). Microbial Ecology 88 (1), 23.

Carlson, C.J., Burgio, KR., Dougherty, E. R., Phillips, A.J., Bueno, V.M., Clements, C.F., et al, 2017. Parasite biodiversity faces extinction and redistribution in a changing climate. Science Advances 3 (9), e1602422.

Carlson, C.J., Hopkins, S., Bell, K.C., Doña, J., Godfrey, S.S., Kwak, M.L., et al, 2020. A global parasite conservation plan. Biological Conservation 250, 108596.

Cazabonne, J., Martin, T.E., Matthews, T.J., Quandt, C.A., Wayman, J.P., Haelewaters, D., 2025. Knowledge gaps explored for Laboulbeniomycetes, a clade of understudied microfungi, including a new shortfall related to a lack of taxonomic expertise. Authorea. https://doi.org/10.22541/au.173956895.54632274/v2

Chatton, E., Picard, F., 1909. Contribution à l'étude systématique et biologique des Laoulbéniacées: *Trenomyces histophtorus* Chatton et Picard, endoparasite des poux de la poule domestique. Bulletin de la Société Mycologique de France 25, 147-170.

Chomel, B.B., Boulouis, H.J., Chang, C.C., Setién, A.A., Stuckey, M.J., 2023. Bat-related zoonoses. In: Sing, A. (Ed.), Zoonoses: Infections Affecting Humans and Animals. Cham: Springer International Publishing, pp. 1035–1070.

Claerhoudt, R., 2024. The legal protection of animal parasites in international biodiversity law. Journal of Environmental Law 36 (3), 301–322.

Colwell, R.K., Dunn, R.R., Harris, N.C., 2012. Coextinction and persistence of dependent species in a changing world. Annual Review of Ecology, Evolution, and Systematics 43 (1), 183–203.

Cuadros-Orellana, S., Leite, L. R., Smith, A., Medeiros, J. D., Badotti, F., Fonseca, P. L., et al, 2013. Assessment of fungal diversity in the environment using metagenomics: a decade in review. Fungal Genomics & Biology 3 (2), 1.

Curran, M., Kopp, M., Ruedi, M., Bayliss, J., 2022. A new species of horseshoe bat (Chiroptera: Rhinolophidae) from Mount Namuli, Mozambique. Acta Chiropterologica 24 (1), 19-40.

da Silva Reis, A., de Almeida Zampaulo, R., de Oliveira Bernardi, L.F., Talamoni, S.A., 2019. *Monunguis streblida* (Neothrombidiidae) in Brazil and its parasitic relationships with dipteran ectoparasites (*Anastrebla* and *Trichobius*) of bats. Parasitology Research 118 (9), 2467–2473.

Dansereau, G., Braga, J., Ficetola, G.F., Galiana, N., Gravel, D., Maiorano, L., et al, 2025. Overcoming the disconnect between species interaction networks and biodiversity conservation. Trends in Ecology & Evolution 40 (9), 840–851. https://doi.org/10.1016/j.tree.2025.05.010

de Bello, F., Fischer, F. M., Puy, J., Shipley, B., Verdú, M., Götzenberger, L., et al, 2025. Raunkiæran shortfalls: Challenges and perspectives in trait-based ecology. Ecological Monographs 95 (2), e70018. https://doi.org/10.1002/ecm.70018

de Groot, M. D., Dumolein, I., Hiller, T., Sándor, A. D., Szentiványi, T., Schilthuizen, M., et al, 2020. On the fly: tritrophic associations of bats, bat flies, and fungi. Journal of Fungi 6 (4), 361.

de Groot, M. D., Santamaria, B., Adriaens, T., Cottrell, T. E., Maes, D., Sakaki, S., et al, 2025. Effects of temperature and humidity on the presence and prevalence of a common fungal parasite on an invasive ladybird. Ecological Entomology 51 (1), 86–97. https://doi.org/10.1111/een.70014

de Sassi, C., Lewis, O.T., Tylianakis, J.M., 2012. Plant-mediated and nonadditive effects of two global change drivers on an insect herbivore community. Ecology 93 (8), 1892–1901.

Dhivahar, J., Parthasarathy, A., Krishnan, K., Kovi, B.S., Pandian, G. N., 2023. Bat-associated microbes: Opportunities and perils, an overview. Heliyon 9 (12).

Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besancon, C., Butt, N., et al, 2017. Changing trends and persisting biases in three decades of conservation science. Global Ecology and Conservation 10, 32–42.

Dick, C.W., 2007. High host specificity of obligate ectoparasites. Ecological Entomology 32 (5), 446–450. https://doi.org/10.1111/j.1365-2311.2006.00836.x

Dick, C.W., Dittmar, K., 2014. Parasitic bat flies (Diptera: Streblidae and Nycteribiidae): host specificity and potential as vectors. In: Klimpel, S., Mehlhorn, H. (Eds.), Bats (Chiroptera) as vectors of diseases and parasites: Facts and myths. Berlin: Springer, pp. 131–155. https://doi.org/10.1007/978-3-642-39333-4_6

Dick, C.W., Graciolli, G., 2018. Checklist of world Streblidae (Diptera: Hippoboscoidea). Chicago: Field Museum of Natural History.

Dick, C. W., Patterson, B.D., 2006. Bat flies: obligate ectoparasites of bats. In: Morand, S., Krasnov, B., Poulin, R. (Eds.) Micromammals and macroparasites: from evolutionary ecology to management. Tokyo: Springer Japan, pp. 179–194.

Dittmar, K., Dick, C.W., Patterson, B.D., Whiting, M.F., Gruwell, M.E., 2009. Pupal deposition and ecology of bat flies (Diptera: Streblidae): Trichobius sp.(caecus group) in a Mexican cave habitat. Journal of Parasitology 95 (2), 308-314. https://doi.org/10.1645/GE-1664.1.

Dittmar, K., Morse, S.F., Dick, C.W., Patterson, B.D., 2015. Bat fly evolution from the Eocene to the present (Hippoboscoidea, Streblidae and Nycteribiidae). In: Morand, S., Krasnov B.R., Littlewood, D.T.J. (Eds.) Parasite diversity and diversification: evolutionary ecology meets phylogenetics. Cambridge University Press, pp. 246-264.

Dogonniuck, A.E., Squires, T.J., Weir, A., 2019. Studies on Dimorphomyceteae: I. New species of Nycteromyces and Dimeromyces (Laboulbeniales) on bat flies (Streblidae). Mycologia 111 (1), 118-126.

Dondini, G., Vergari, S., Mori, E., Bertonelli, S., Ancillotto, L., 2025. Are bats tracking climate change? Long-term monitoring reveals phenology shifts and population trends of forest bats. Science of The Total Environment 969, 178995.

Dougherty, E. R., Carlson, C. J., Bueno, V. M., Burgio, K. R., Cizauskas, C. A., Clements, C. F., et al, 2016. Paradigms for parasite conservation. Conservation biology 30 (4), 724-733.

Duchamp, J.E., Swihart, R.K., 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. Landscape Ecology 23 (7), 849-860.

Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P., Sodhi, N.S., 2009. The sixth mass coextinction: are most endangered species parasites and mutualists?. Proceedings of the Royal Society B: Biological Sciences 276 (1670), 3037-3045.

Eber, S., 2001. Multitrophic interactions: the population dynamics of spatially structured plant-herbivore-parasitoid systems. Basic and Applied Ecology 2 (1), 27-33.

Ekanayaka, A. H., Karunarathna, S. C., Tibpromma, S., Dutta, A. K., Tennakoon, D. S., Karunarathna, A., et al, 2025. Species evolution: cryptic species and phenotypic noise with a particular focus on fungal systematics. Frontiers in Cellular and Infection Microbiology 15, 1497085.

Eriksson, A., Filion, A., Labruna, M.B., Muñoz-Leal, S., Poulin, R., Fischer, E., et al, 2023. Effects of forest loss and fragmentation on bat-ectoparasite interactions. Parasitology Research 122 (6), 1391-1402.

Essl, F., Dullinger, S., Rabitsch, W., Burns, K. C., Foufopoulos, J., Hulme, P. E., et al, 2026. Dark extinctions warrant recognition in Red Lists. Nature Reviews Biodiversity, 1-3.

Festa, F., Ancillotto, L., Santini, L., Pacifici, M., Rocha, R., Toshkova, N., et al, 2023. Bat responses to climate change: a systematic review. Biological Reviews 98 (1), 19-33.

Findley, J. S., 1995. Bats: a community perspective. Cambridge University Press.

Frick, W.F., Kingston, T., Flanders, J., 2020. A review of the major threats and challenges to global bat conservation. Annals of the new York Academy of Sciences 1469 (1), 5-25.

Furlong, M.J., Pell, J.K., 2005. Interactions between entomopathogenic fungi and other arthropods natural enemies. In: Vega, F.E., Blackwell, M. (Eds.) Insect-fungal associations, ecology and evolution. Oxford: Oxford University Press, pp. 51-73.

Gagne, R. B., Crooks, K. R., Craft, M. E., Chiu, E. S., Fountain-Jones, N. M., Malmberg, J. L., et al, 2022. Parasites as conservation tools. Conservation Biology 36 (1), e13719.

Galbreath, K. E., Hoberg, E. P., Cook, J. A., Armién, B., Bell, K. C., Campbell, M. L., et al, 2019. Building an integrated infrastructure for exploring biodiversity: field collections and archives of mammals and parasites. Journal of Mammalogy 100 (2), 382-393.

García-Morales, R., Badano, E.I., Moreno, C.E., 2013. Response of Neotropical bat assemblages to human land use. Conservation Biology 27 (5), 1096–1106. https://doi.org/10.1111/cobi.12099

Gleason, F.H., Lilje, O., Marano, A.V., Sime-Ngando, T., Sullivan, B.K., Kirchmair, M., Neuhauser, S., 2014. Ecological functions of zoosporic hyperparasites. Frontiers in Microbiology 5, 244.

Goldberg, T.L., Bennett, A.J., Kityo, R., Kuhn, J.H., Chapman, C.A., 2017. Kanyawara virus: a novel rhabdovirus infecting newly discovered nycteribiid bat flies infesting previously unknown pteropodid bats in Uganda. Scientific Reports 7(1), 5287.

Goldmann, L., Weir, A., 2012. Position specificity in Chitonomyces (Ascomycota, Laboulbeniomycetes) on Laccophilus (Coleoptera, Dytiscidae): a molecular approach resolves a century-old debate. Mycologia 104(5), 1143-1158.

Graciolli, G., Dick, C.W., 2018. Checklist of World Nycteribiidae (Diptera: Hippoboscoidea). Field Museum of Natural History, Chicago.

Grunwald, A.L., Demos, T.C., Nguéagni, Y., Tchamba, M.N., Monadjem, A., Webala, P.W., .et al, 2023. A review of bats of the genus Pseudoromicia (Chiroptera: Vespertilionidae) with the description of a new species. Systematics and Biodiversity 21 (1), 2156002.

Haelewaters, D., Blackwell, M., Pfister, D.H., 2021a. Laboulbeniomycetes: intimate fungal associates of arthropods. Annual Review of Entomology 66, 257-276. https://doi.org/10.1146/annurev-ento-013020-013553.

Haelewaters, D., Hiller, T., Dick, C.W., 2018. Bats, bat flies, and fungi: a case of hyperparasitism. Trends in Parasitology 34 (9), 784-799.

Haelewaters, D., Dima, B., Abdel-Hafiz, A.I., Abdel-Wahab, M.A., Abul-Ezz, S.R., Acar, I., et al, 2020. Fungal systematics and evolution 6. Sydowia 72, 231–356.

Haelewaters, D., Dick, C.W., Cocherán Pittí, K.P., Dittmar, K., Patterson, B.D., 2021b. Bats, bat flies, and fungi: Exploring uncharted waters. In: Lim, B.K., Fenton, M.B., Brigham, R.M., Mistry, S., Kurta, A., Gillam, E.H., Russell, A. & Ortega, J. (Eds.) 50 years of bat research. Fascinating Life Sciences. Springer, Cham., pp. 349–371. https://doi.org/10.1007/978-3-030-54727-1_21

Haelewaters, D., Schoutteten, N., Medina-van Berkum, P., Martin, T. E., Verbeken, A., Aime, M.C., 2021c. Pioneering a fungal inventory at Cusuco National Park, Honduras. Journal of Mesoamerican Biology 1 (1).

Haelewaters, D., Lubbers, M., De Kesel, A., 2022a. The haustorium as a driving force for speciation in thallus-forming Laboulbeniomycetes. IMA fungus 13 (1), 1-8. https://doi.org/10.1186/s43008-021-00087-7

Haelewaters, D., Matthews, J., Wayman, J. P., Cazabonne, J., Heyman, F., Quandt, C.A., Martin, T.E., 2024a. Biological knowledge shortfalls impede conservation efforts in poorly studied taxa—A case study of Laboulbeniomycetes. Journal of Biogeography 51 (1), 29-39.

Haelewaters, D., Hughes, M., Barão-Nóbrega, J.A.L., Slater, K., Martin, T.E., 2024b. Standard deviation: Standardized bat monitoring techniques work better in some ecosystems. Plos one 19 (12), e0311553.

Haelewaters, D., Pfliegler, W. P., Gorczak, M., Pfister, D.H., 2019. Birth of an order: comprehensive molecular phylogenetic study excludes Herpomyces (Fungi, Laboulbeniomycetes) from Laboulbeniales. Molecular phylogenetics and evolution 133, 286-301. https://doi.org/10.1016/j.ympev.2019.01.007

HHaelewaters, D., Pfliegler, W. P., Szentiványi, T., Földvári, M., Sándor, A. D., Barti, L., et al, 2017a. Parasites of parasites of bats: Laboulbeniales (Fungi: Ascomycota) on bat flies (Diptera: Nycteribiidae) in central Europe. Parasites & Vectors 10 (1), 1-14. https://doi.org/10.1186/s13071-017-2022-y

Haelewaters, D., Pfister, D.H., 2019. Morphological species of Gloeandromyces (Ascomycota, Laboulbeniales) evaluated using single-locus species delimitation methods. Fungal Systematics and Evolution 3 (1), 19-34. https://doi.org/10.3114/fuse.2019.03.03

Haelewaters, D., Okrasińska, A., Gorczak, M., Pfister, D.H., 2020. Draft genome sequence of the globally distributed cockroach-infecting fungus Herpomyces periplanetae strain D. Haelew. 1187d. Microbiology Resource Announcements 9 (6), 10-1128.

Haelewaters, D., Verhaeghen, S.J., Rios Gonzalez, T.A., Bernal Vega, J.A., Villarreal Saucedo, R.V., 2017b. New and interesting Laboulbeniales from Panama and neighboring areas. Nova Hedwigia 105(3-4), 267-299. https://doi.org/10.1127/nova_hedwigia/2017/0410

Haelewaters, D., Zhao, S.Y., Clusella-Trullas, S., Cottrell, T.E., De Kesel, A., Fiedler, L., et al, 2017c. Parasites of Harmonia axyridis: current research and perspectives. BioControl 62 (3), 355-371.

Haelewaters, D., Aghayeva, D., De-Miguel, S., Degtjarenko, P., Dierickx, G., Dima, B., et al, 2026a. Mapping the landscape of mycological organizations in europe: where citizen science meets professional mycology. Biodiversity and Conservation 35 (1), 37.

Haelewaters, D., De Wint, F.C., Gorczak, M., Hessmann, D., Jensen, A.B., Francis, F., et al, 2026b. Ecology and management perspectives in arthropod–fungal associations. Authorea. https://doi.org/10.22541/au.177032832.23372849/v1

Hatcher, M. J., Dick, J. T., Dunn, A.M., 2012. Diverse effects of parasites in ecosystems: linking interdependent processes. Frontiers in Ecology and the Environment 10 (4), 186-194.

Hawksworth, D. L., Rossman, A.Y., 1997. Where are all the undescribed fungi?. Phytopathology 87 (9), 888-891.

Hayes, M. A., Adams, R.A., 2017. Simulated bat populations erode when exposed to climate change projections for western North America. PLoS One 12 (7), e0180693.

Heinen, J.H., Rahbek, C., Borregaard, M.K., 2020. Conservation of species interactions to achieve self-sustaining ecosystems. Ecography 43 (11), 1603-1611.

Heleno, R., Devoto, M., Pocock, M., 2012. Connectance of species interaction networks and conservation value: is it any good to be well connected?. Ecological indicators 14 (1), 7-10.

Herrera, J.P., Moody, J., Nunn, C.L., 2021. Predictions of primate–parasite coextinction. Philosophical Transactions of the Royal Society B: Biological Sciences 376 (1837).

Hiller, T., Brändel, S.D., Honner, B., Page, R.A., Tschapka, M., 2020. Parasitization of bats by bat flies (Streblidae) in fragmented habitats. Biotropica 52 (3), 488-501.

Hiller, T., Honner, B., Page, R.A., Tschapka, M., 2018. Leg structure explains host site preference in bat flies (Diptera: Streblidae) parasitizing neotropical bats (Chiroptera: Phyllostomidae). Parasitology 145 (11), 1475-1482.

Hopkins, S., Kwak, M., 2023. New IUCN Species Survival Commission Parasite Specialist Group launched in 2023. Oryx 57 (3), 283-283.

Hopkins, S., Kwak, M., 2024. 2023 Report of the Parasite Specialist Group. In: IUCN SSC and Secretariat. 2023 Report of the IUCN Species Survival Commission and Secretariat. Gland, Switzerland: IUCN. pp. 4.

Hopkins S.R., Wood C.L., 2026. Parasite conservation now: turning knowledge into action. Trends in Parasitology ISSN 1471-4922. https://doi.org/10.1016/j.pt.2026.03.009.

Hoyt, J.R., Kilpatrick, A.M., Langwig, K.E., 2021. Ecology and impacts of white-nose syndrome on bats. Nature Reviews Microbiology 19 (3), 196-210. https://doi.org/10.1038/s41579-020-00493-5

Hrycyna, G., Santos, C.L.D., Rebêlo, J.M., Graciolli, G., 2022. A New Species of Hershkovitzia (Diptera: Nycteribiidae) from Maranhão, Brazil. Anais da Academia Brasileira de Ciências 94 (1), e20191161.

Huang, G., Liu, X., Huang, X., Gao, C., Wang, Z., Li, J., et al, 2025. Adaptive evolution of traits for parasitism and pathogen transmission potential in bat flies. National Science Review 12 (3), nwae245.

Hudson, P.J., Dobson, A.P., Lafferty, K.D., 2006. Is a healthy ecosystem one that is rich in parasites?. Trends in ecology & evolution 21 (7), 381-385.

Hussain, M., Ali, W., Meyer, C.F.J., Javid, A., Imran, M., 2025. Roost site selection and seasonal dynamics of the Indian flying fox (Pteropus medius): Influence of environmental and anthropogenic factors. Biosystems Diversity 33 (3), e2546-e2546.

Ingala de Waal, M., Oliveira, H., Frank, L.E., Hussain, M., Kazam, A., Becker, D.J., et al, 2025. Bats in habitats, bats as habitats: Integrating synergistic ecological interactions across levels of community organization. EcoEvoRxiv. https://doi.org/10.32942/X2RW59

Irga, P.J., Dominici, L., Torpy, F.R., 2020. The mycological social network a way forward for conservation of fungal biodiversity. Environmental Conservation 47 (4), 243-250.

IUCN, 2026. The IUCN Red List of Threatened Species. Version 2025-2. https://www.iucnredlist.org. Accessed on 10 may 2026.

Joop, G., Vilcinskas, A., 2016. Coevolution of parasitic fungi and insect hosts. Zoology, 119(4), 350-358.

Kaishian, P. J. (2021). Insects and their Laboulbeniales (Ascomycota, Fungi) of Lake Eustis and Emeralda Marsh Conservation Area: A case study on urbanization and diversity. Ecology and Evolution 11 (23), 16618-16633. https://doi.org/10.1002/ece3.8246

Kark, S., Tulloch, A., Gordon, A., Mazor, T., Bunnefeld, N., Levin, N., 2015. Cross-boundary collaboration: key to the conservation puzzle. Current Opinion in Environmental Sustainability 12, 12-24.

Koga, R., Moriyama, M., Nozaki, T., Fukatsu, T., 2024. Genome analysis of “Candidatus Aschnera chinzeii,” the bacterial endosymbiont of the blood-sucking bat fly Penicillidia jenynsii (Insecta: Diptera: Nycteribiidae). Frontiers in microbiology 14, 1336919.

Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S., 2004. Species coextinctions and the biodiversity crisis. science 305 (5690), 1632-1634.

Kolenati, F.A., 1857. Epizoa der Nycteribien. Wien Entomol Monatsschr 1, 66-9.

Korine, C., Adams, R., Russo, D., Fisher-Phelps, M., Jacobs, D., 2016. Bats and water: anthropogenic alterations threaten global bat populations. Bats in the Anthropocene: Conservation of bats in a changing world 8, 215-241.

Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., De Leo, G., Dobson, A.P., et al, 2008. Parasites in food webs: the ultimate missing links. Ecology letters 11 (6), 533-546.

Lafferty, K.D., 2012. Biodiversity loss decreases parasite diversity: theory and patterns. Philosophical Transactions of the Royal Society B: Biological Sciences 367 (1604), 2814-2827.

Lafferty, K.D., Dobson, A.P., Kuris, A.M., 2006. Parasites dominate food web links. Proceedings of the National Academy of Sciences 103 (30), 11211-11216.

Lee, H., Seo, M.G., Lee, S.H., Oem, J.K., Kim, S.H., Jeong, H., et al, 2021. Relationship among bats, parasitic bat flies, and associated pathogens in Korea. Parasites & Vectors 14 (1), 503.

Li, C. H., Wang, Y.R., Lesack, K., Xiao, X., Pollo, S. M., Jonsdottir, T. K., et al, 2025. Perceptions of parasites: reflections from a new parasitology outreach initiative. Trends in Parasitology 41, 509-513.

Lindquist, E.E., Vercammen-Grandjean, P.H., 1971. Revision of the chiggerlike larvae of the genera Neotrombidium Leonardi and Monunguis Wharton, with a redefinition of the subfamily Neotrombidiinae Feider in the Trombidiidae (Acarina: Prostigmata) 1. The Canadian Entomologist 103 (11), 1557-1590.

Liu, J., Haelewaters, D., Pfliegler, W.P., Page, R.A., Dick, C.W., Aime, M.C., 2020. A new species of Gloeandromyces from Ecuador and Panama revealed by morphology and phylogenetic reconstruction, with a discussion of secondary barcodes in Laboulbeniomycetes taxonomy. Mycologia 112 (6), 1192-1202.

López-Rivera, C., Robayo-Sánchez, L. N., Ramírez-Hernández, A., Cortés-Vecino, J. A., Cuéllar-Sáenz, J. A., Villar, J. D., et al, 2024. Hyperparasitism in bat flies (Diptera: Streblidae): new records and interaction networks in the Neotropics. Parasitology Research 123 (6), 255.

Lubbers, M., Lamers, G.E.M., De Kesel, A., Nedvěd, O., Schilthuizen, M., Haelewaters, D., 2022. Bacterial biofilms on thalli of Laboulbeniales: a community uncovered. Sydowia 74, 335–342. https://doi.org/10.12905/0380.sydowia74-2022-0335

Lučan, R. K., Bandouchova, H., Bartonička, T., Pikula, J., Zahradníková Jr, A., Zukal, J., Martínková, N., 2016. Ectoparasites may serve as vectors for the white-nose syndrome fungus. Parasites & Vectors 9 (1), 16.

Lücking, R., Aime, M.C., Robbertse, B., Miller, A.N., Aoki, T., Ariyawansa, H.A., et al, 2021. Fungal taxonomy and sequence-based nomenclature. Nature microbiology 6 (5), 540-548.

Lymbery, A.J., Lymbery, S.J., 2024. Equal rights for parasites: Are we there yet?. International Journal for Parasitology: Parasites and Wildlife 24, 100945.

Lymbery, A.J., Smit, N.J., 2023. Conservation of parasites: a primer. International Journal for Parasitology: Parasites and Wildlife 21, 255-263.

Maharachchikumbura, S.S., Chen, Y., Ariyawansa, H.A., Hyde, K.D., Haelewaters, D., Perera, R.H., et al, 2021. Integrative approaches for species delimitation in Ascomycota. Fungal Diversity 109 (1), 155-179.

Mammola, S., Riccardi, N., Prié, V., Correia, R., Cardoso, P., Lopes-Lima, M., Sousa, R., 2020. Towards a taxonomically unbiased European Union biodiversity strategy for 2030. Proceedings of the Royal Society B 287 (1940), 20202166.

Marcatti, R., Franco, L.A.M., Rocha, E.C., Nardi, M.S., Summa, J.L., da Silva, E.T.B.C., et al, 2025. Metagenomics enables the first detection of Trypanosoma sp. in Streblidae (Diptera: Hippoboscoidea) parasitizing bats in São Paulo, Brazil. Frontiers in Systems Biology 5, 1721019.

Marshall, A.G., 1982. Ecology of insects ectoparasitic on bats. Ecology of bats, 369-401.

Marjakangas, E.L., Muñoz, G., Turney, S., Albrecht, J., Neuschulz, E.L., Schleuning, M., Lessard, J.P., 2022. Trait-based inference of ecological network assembly: A conceptual framework and methodological toolbox. Ecological Monographs 92 (2), e1502.

Meiners, T., 2015. Chemical ecology and evolution of plant–insect interactions: a multitrophic perspective. Current Opinion in Insect Science 8, 22-28.

Merola, A., 1952. Interessante ritrovamento di labulbeniologia cavernicola: Arthrorhynchus acrandros n. sp. (con considerazioni sul gen. Arthrorhynchus). Bollettino della Società dei naturalisti in Napoli 60, 1-30.

Meyer, C.F., Struebig, M.J., Willig, M.R., 2016. Responses of tropical bats to habitat fragmentation, logging, and deforestation. In: Voigt, C., Kingston, T. (Eds.) Bats in the Anthropocene: conservation of bats in a changing world. Springer, Cham., pp. 63-103.

Mickleburgh, S.P., Hutson, A.M., Racey, P.A., 2002. A review of the global conservation status of bats. Oryx 36 (1), 18-34.

Minter, D.W., 2011. What every botanist and zoologist should know-and what every mycologist should be telling them. IMA fungus 2 (1).

Moreno Santillan, D.D., Lama, T.M., Gutierrez Guerrero, Y.T., Brown, A.M., Donat, P., Zhao, H., et al, 2021. Large-scale genome sampling reveals unique immunity and metabolic adaptations in bats. Molecular ecology 30 (23), 6449-6467.

Nguyen, T., Malina, R., Mokas, I., Papakonstantinou, A., Polyzos, O., Vanhove, M.P., 2023. WASP: the World Archives of Species Perception. Database 2023, baad003.

Niskanen, T., Lücking, R., Dahlberg, A., Gaya, E., Suz, L.M., Mikryukov, V., .et al, 2023. Pushing the frontiers of biodiversity research: Unveiling the global diversity, distribution, and conservation of fungi. Annual review of Environment and resources 48 (1), 149-176.

Nosawad, A., 1973. *Arthrorhynchus nycteribiae* (Peyritsch) Thaxter (Ascomycetes, Laboulbeniales) w Polsce. Pol. P. Entomol. 43, 423-430.

Novaes, R.L.M., Cláudio, V.C., Carrión-Bonilla, C., Abreu, E.F., Wilson, D.E., Maldonado, J.E., Weksler, M., 2022. Variation in the Myotis keaysi complex (Chiroptera, Vespertilionidae), with description of a new species from Ecuador. Journal of Mammalogy 103 (3), 540-559.

Okamura, B., Hartigan, A., Naldoni, J., 2018. Extensive uncharted biodiversity: the parasite dimension. Integrative and Comparative Biology 58 (6), 1132-1145.

Overal, W.L., 1980. Host-relations of the bat fly Megistopoda aranea (Diptera: Streblidae) in Panama [Restricted to Artibeus jamaicensis]. University of Kansas Science Bulletin 52 (1), 1-20.

Ozman-Sullivan, S.K., Sullivan, G.T., 2023. Coextinction is magnifying the current extinction crisis, as illustrated by the eriophyoid mites and their host plants. Acarologia 63 (1), 169-179.

Palheta, L.R., Urbieta, G.L., Brasil, L.S., Dias-Silva, K., Da Silva, J.B., Graciolli, G., et al, 2020. The effect of urbanization on bats and communities of bat flies (Diptera: Nycteribiidae and Streblidae) in the Amazon, northern Brazil. Acta Chiropterologica 22 (2), 403-416.

Patrício, P.M.P., Lourenço, E.C., Freitas, A.Q.D., Famadas, K.M., 2016. Host morphophysiological conditions and environment abiotic factors correlate with bat flies (Streblidae) prevalence and intensity in Artibeus Leach, 1821 (Phyllostomidae). Ciência Rural 46 (4), 648-653.

Pedersen, A.B., Fenton, A., 2007. Emphasizing the ecology in parasite community ecology. Trends in ecology & evolution 22 (3), 133-139.

Péter, Á., Mihalca, A.D., Haelewaters, D., Sándor, A.D., 2022. Focus on hyperparasites: biotic and abiotic traits affecting the prevalence of parasitic microfungi on bat ectoparasites. Frontiers in Ecology and Evolution 10, 795020.

Pilosof, S., Dick, C.W., Korine, C., Patterson, B.D., Krasnov, B.R., 2012. Effects of anthropogenic disturbance and climate on patterns of bat fly parasitism. PloS one 7 (7), e41487.

Płoszka, Z., Nowak, K.H., Tischer, M., Michalik, A., Kolasa, M.R., Łukasik, P., 2025. Dissecting multitrophic interactions: The relationships among Entomophthora, their dipteran hosts, and associated bacteria. Journal of Invertebrate Pathology, 108425.

Porter, M.L., Lutz, H., Steck, M., Chong, R.A., 2022. The complete mitochondrial genomes and phylogenetic analysis of two Nycteribiidae bat flies (Diptera: Hippoboscoidea). Mitochondrial DNA Part B 7 (8), 1486-1488.

Poulin, R., 2010. Network analysis shining light on parasite ecology and diversity. Trends in parasitology 26 (10), 492-498.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., .et al, 1996. Challenges in the quest for keystones: identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. BioScience 46 (8), 609-620.

Ramasindrazana, B., Goodman, S.M., Gomard, Y., Dick, C.W., Tortosa, P., 2017. Hidden diversity of Nycteribiidae (Diptera) bat flies from the Malagasy region and insights on host-parasite interactions. Parasites & Vectors 10 (1), 630.

Ramírez-Fráncel, L.A., García-Herrera, L.V., Losada-Prado, S., Reinoso-Flórez, G., Sánchez-Hernández, A., Estrada-Villegas, L.B.K., Guevara, G., 2022. Bats and their vital ecosystem services: a global review. Integrative Zoology 17 (1): 223. https://doi.org/10.1111/1749-4877.12552

Ramírez-Martínez, M.M., Bennett, A.J., Dunn, C.D., Yuill, T.M., Goldberg, T.L., 2021. Bat flies of the family Streblidae (Diptera: Hippoboscoidea) host relatives of medically and agriculturally important “bat-associated” viruses. Viruses 13 (5), 860.

Razak, N.A., Gange, A.C., 2023. Multitrophic interactions between arbuscular mycorrhizal fungi, foliar endophytic fungi and aphids. Microbial ecology 85 (1), 146-156.

Reboleira, A.S.P.S., Moritz, L., Santamaria, S., Enghoff, H., 2021. Penetrative and non-penetrative interaction between Laboulbeniales fungi and their arthropod hosts. Scientific Reports 11, 22170. https://doi.org/10.1038/s41598-021-01729-x

Riley, C.V., 1892. The yucca moth and yucca pollination. Missouri Botanical Garden.

Roberge, J.M., Angelstam, P.E.R., 2004. Usefulness of the umbrella species concept as a conservation tool. Conservation biology 18 (1), 76-85.

Rocha, C.F.D., Bergallo, H.G., Bittencourt, E.B., 2016. More than just invisible inhabitants: parasites are important but neglected components of the biodiversity. Zoologia (Curitiba) 33 (03), e20150198.

Roy, H.E., Steinkraus, D.C., Eilenberg, J., Hajek, A.E., Pell, J.K., 2006. Bizarre interactions and endgames: entomopathogenic fungi and their arthropod hosts. Annual review of entomology 51 (1), 331-357.

Runge, C.A., Withey, J.C., Naugle, D.E., Fargione, J.E., Helmstedt, K.J., Larsen, A.E., et al, 2019. Single species conservation as an umbrella for management of landscape threats. PLoS One 14 (1), e0209619.

Runghen, R., Poulin, R., Monlleó-Borrull, C., Llopis-Belenguer, C., 2021. Network analysis: ten years shining light on host–parasite interactions. Trends in Parasitology 37 (5), 445-455.

Ryberg. O., 1947. Studies on bats and bat parasites, especially with regard to Sweden and other neighbouring countries of the north. I. Bokfrlaget Svensk Natur, Stockholm.

Rynkiewicz, E.C., Pedersen, A.B., Fenton, A., 2015. An ecosystem approach to understanding and managing within-host parasite community dynamics. Trends in parasitology 31 (5), 212-221.

Saikia, U., Chakravarty, R., Csorba, G., Laskar, M.A., Ruedi, M., 2025. Taxonomic reassessment of bats from the Western Himalayas, India and description of a new species of the Myotis frater complex (Mammalia, Chiroptera, Vespertilionidae). Zootaxa 5644 (1), 1-78.

Salinas-Ramos, V.B., Zaldívar-Riverón, A., Rebollo-Hernández, A., Herrera-M, L.G., 2018. Seasonal variation of bat-flies (Diptera: Streblidae) in four bat species from a tropical dry forest. Mammalia 82 (2), 133-143.

Sebastián Tello, J., Stevens, R.D., Dick, C.W., 2008. Patterns of species co-occurrence and density compensation: a test for interspecific competition in bat ectoparasite infracommunities. Oikos 117 (5), 693-702.

Sherwin, H.A., Montgomery, W.I., Lundy, M.G., 2012. The impact and implications of climate change for bats. Mammal Review 43 (3), 171-182.

Simmons, N.B., Cirranello, A.L., 2025. Bat Species of the World: A taxonomic and geographic database. Version 1.9. Accessed on 03/05/2026.

Speer, K.A., Dheilly, N.M., Perkins, S.L., 2020. Microbiomes are integral to conservation of parasitic arthropods. Biological Conservation 250, 108695.

Stallman, J. K., Haelewaters, D., Koch Bach, R. A., Brann, M., Fatemi, S., Gomez-Zapata, P., .et al, 2024. The contribution of tropical long-term studies to mycology. IMA fungus 15 (1), 35.

Stengel, A., Stanke, K.M., Quattrone, A.C., Herr, J.R., 2022. Improving taxonomic delimitation of fungal species in the age of genomics and phenomics. Frontiers in microbiology 13, 847067.

Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on Earth?. Annual review of entomology 63 (2018), 31-45.

Strona, G., 2015. Past, present and future of host–parasite co-extinctions. *I*nternational Journal for Parasitology: Parasites and Wildlife 4 (3), 431-441.

Sullivan, D.J., 2009. Hyperparasitism. In: Vincent, H. Resh, V.H., Cardé, R.T. (Eds.) Encyclopedia of insects. Academic Press, pp. 486-488.

Sullivan, D.J., Völkl, W., 1999. Hyperparasitism: multitrophic ecology and behavior. Annual review of entomology 44 (1), 291-315.

Szentiványi, T., Christe, P., Glaizot, O., 2019. Bat flies and their microparasites: current knowledge and distribution. Frontiers in Veterinary Science 6, 115.

Szentiványi, T., Estók, P., 2024. Penicillidia conspicua. Trends in Parasitology 40 (2), 194-195.

Szopieray, K., Żbikowska, E., 2021. Positive role of parasites. Acta Zoologica Academiae Scientiarum Hungaricae 67 (3), 289-300.

Thaxter, R., 1901. Preliminary diagnosis of new species of Laboulbeniaceae. III. Proceedings of the American Academy of Arts and Sciences 36, 397-414.

Thaxter, R., 1917. New Laboulbeniales, chiefly dipterophilous American species. Proceedings of the American Academy of Arts and Sciences 52, 649–721. https://doi.org/10.2307/20025703

Thaxter, R. 1926. Contribution towards a monograph of the Laboulbeniaceae. Part IV. Memoirs of the American Academy of Arts and Sciences 15: 427-580, Plates I-XXIV.

Thaxter R., 1931. Contribution towards a monograph of the Laboulbeniaceae. Part V. Memoirs of the American Academy of Arts and Sciences 16, 1-435.

Thomas-Walters, L., Raihani, N.J., 2017. Supporting conservation: The roles of flagship species and identifiable victims. Conservation Letters 10 (5), 581-587.

Tlapaya-Romero, L., Santos-Moreno, A., Ibáñez-Bernal, S., 2021. Effect of seasonality and microclimate on the variation in bat-fly load (Diptera: Streblidae) in a cave bat assemblage in a dry forest. Mammalia 85 (4), 345-354.

Tlapaya-Romero, L., García-Méndez, A., Ramírez-Martínez, M.M., 2023. A new species of Trichobius (Diptera: Streblidae) from Mexico and new record of Paratrichobius americanus. Systematic Parasitology 100 (1), 59-67.

Torchin, M.E., Miura, O., Hechinger, R.F., 2015. Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts. Ecology 96 (11), 3033-3042.

Truter, M., Schaeffner, B.C., Smit, N.J., 2025. Aquatic parasite conservation. In: Smit, N.J., Sures, B. (Eds.) Aquatic Parasitology: Ecological and Environmental Concepts and Implications of Marine and Freshwater Parasites. Cham: Springer Nature Switzerland, pp. 325-360.

Tscharntke, T., Hawkins, B.A., 2002. Multitrophic level interactions. Cambridge University Press.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecology letters 11 (12), 1351-1363.

Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. Biological conservation 143 (10), 2270-2279.

Tyson, R., Haines, S., Hodges, K.E., 2010. Modelling the Canada lynx and snowshoe hare population cycle: the role of specialist predators. Theoretical Ecology 3 (2), 97-111.

Van Caenegem, W., Blondelle, A., Dumolein, I., Santamaria, B., Dick, C.W., Hiller, T., et al, 2023. Five new species of Gloeandromyces (Fungi, Laboulbeniales) from tropical American bat flies (Diptera, Streblidae), revealed by morphology and phylogenetic reconstruction. Mycologia 115 (5), 714-737.

Van Caenegem, W., Montalva, C., Rojas, E., Beuk, P.L.Th., De Kesel, A., Verbeken, A., Haelewaters, D., 2026. A discussion on the genus *Stigmatomyces* sensu lato and the description of two new species from Chile. Mycologia, 1–21.

Van de Vuurst, P., Gohlke, J. M., Escobar, L.E., 2025. Future climate change and the distributional shift of the common vampire bat, Desmodus rotundus. Scientific Reports 15 (1), 5989.

Vega, F.E., Blackwell, M., 2005. Insect-fungal associations: ecology and evolution. Oxford University Press.

Walther, G.R., 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B: Biological Sciences 365 (1549), 2019-2024.

Wang, X., Han, X., Csorba, G., Wu, Y., Chen, H., Zhao, X., et al, 2025. A new species of tube-nosed bat (Chiroptera: Vespertilionidae: Murina) from Qinghai–Tibet Plateau, China. Journal of Mammalogy 106 (1), 178-186.

Wang, Y., Insuk, C., Olson, C., Xu, J., 2026. Metagenomic and Genomic Analyses Reveal Prevalent Spread and Evolution of the Bat White-Nose Pathogen Pseudogymnoascus destructans in Western Canada. Journal of Fungi 12 (2), 154.

Weir, A., 2004. The Laboulbeniales—an enigmatic group of arthropod-associated fungi. In: Seckbach, J. (Ed.) Symbiosis: Mechanisms and Model Systems. Dordrecht: Springer Netherlands, pp. 611-620.

Weir, A., Hammond, P.M., 1997. Laboulbeniales on beetles: Host utilization patterns and species richness of the parasites. Biodiversity and Conservation 6, 701–719. https://doi.org/10.1023/A:1018318320019

Windsor, D.A., 1997. Equal rights for parasites. Perspectives in biology and medicine 40 (2), 222-229.

Wolinska, J., King, K.C., 2009. Environment can alter selection in host–parasite interactions. Trends in parasitology 25 (5), 236-244.

Xie, J., De Wint, F.C., Yin, P., El Madani, F., de Groot, M.D., De Clercq, P., Haelewaters, D., 2026. Artificial infection of three ladybird species by the ectoparasitic fungus *Hesperomyces harmoniae*. Biological Control 217, 106047. https://doi.org/10.1016/j.biocontrol.2026.106047

Xu, J., 2006. Microbial ecology in the age of genomics and metagenomics: concepts, tools, and recent advances. Molecular ecology 15 (7), 1713-1731.

Xu, Z., Yang, W., Feng, Y., Li, Y., Fu, S., Li, X., et al, 2019. Isolation and identification of a highly divergent kaeng khoi virus from bat flies (Eucampsipoda sundaica) in China. Vector-Borne and Zoonotic Diseases 19 (1), 73-80.

Yamazaki, I., Onuma, M., Ri, T., Okane, I., Kanzaki, N., Degawa, Y., Sawamura, K., 2023. Laboratory experiments of Stigmatomyces majewskii (Laboulbeniales: Laboulbeniaceae) infection on Drosophila suzukii (Diptera: Drosophilidae). Applied entomology and zoology 58 (4), 379-385.

Zahradníková Jr, A., Kovacova, V., Martínková, N., Orlova, M. V., Orlov, O. L., Piacek, V., et al, 2018. Historic and geographic surveillance of Pseudogymnoascus destructans possible from collections of bat parasites. Transboundary and Emerging Diseases 65 (2), 303-308.

Zhu, H., Zou, X., Wang, D., Wan, S., Wang, L., Guo, J., 2015. Responses of community-level plant-insect interactions to climate warming in a meadow steppe. Scientific Reports 5 (1), 18654.