# Knowledge gaps explored for Laboulbeniomycetes, a clade of understudied microfungi, including a new shortfall related to a lack of taxonomic expertise

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## Abstract

Despite escalating efforts to document and understand biodiversity, gaps in knowledge persist due to the inherent complexity of biological systems and the sheer scale of global biodiversity. Such knowledge shortfalls have been identified, described, and discussed for several well-studied organismal groups, leading to significant advancements in research and conservation. However, less-studied organismal groups (including most fungi) continue to suffer from pronounced knowledge gaps. Recently, Laboulbeniomycetes (phylum Ascomycota), a class of minute fungi obligately associated with arthropods either for dispersal or as epibionts, has been proposed as a model system to illustrate the extent of biodiversity and conservation shortfalls in poorly known organismal groups. Here, we explore biodiversity knowledge shortfalls for the Laboulbeniomycetes, examining gaps in species diversity (Linnean), distribution (Wallacean), populations (Prestonian), evolution (Darwinian), functional traits and ecological functions (Raunkiaeran), abiotic tolerance (Hutchinsonian), ecological interactions (Eltonian), natural history knowledge (Parkerian), persistence (Latimerian), conservation assessment (Scottian), and applied conservation, legal policies, fundings, and public awareness (Ostromian). Additionally, we introduce the Thaxterian shortfall, named after Roland Thaxter (1858–1932), professor at Harvard University and leading expert of Laboulbeniales, that quantifies the lack of taxonomic expertise in a given organismal group. We also discuss the implications of these shortfalls for conservation and future research avenues. We hope this chapter will serve as a catalyst for further discussion on biodiversity shortfalls in other taxa and pave the way towards a global momentum for the integration of poorly known organisms into conservation frameworks.

> *Unlike the majority of fungi which subsist as parasites of living insects, the present group includes none of the conspicuous productions that are so characteristic among entomogenous fungi generally; and their usually minute size doubtless accounts, in some degree, for the fact that, although they are in certain respects among the most important of fungus organisms, they have been so long neglected by botanists and so generally overlooked or disregarded by entomologists.*
>
> – Roland Thaxter (Contribution towards a monograph of the Laboulbeniaceae, 1896)

# Introduction

A comprehensive understanding of biodiversity (and its associated geographical and ecological patterns) remains challenging given its inherent complexity, lacunae in existing theoretical framework, data scarceness, and poor sample sizes (Hortal *et al.*, 2015). Despite increasing efforts to classify organisms and understand their ecology, major knowledge gaps remain, even for well-studied vertebrate groups, as do the challenges associated with filling them (Bini *et al.*, 2006; Scarpignato *et al.*, 2023; Urbina-Cardona *et al.*, 2023). Such shortfalls directly impede conservation efforts, given that fundamental knowledge of biodiversity (including threat statuses, morphological and molecular diversity, geographical distributions, and species interactions) is essential to develop efficient management plans and identify conservation priorities in the face of global change (Cardoso *et al.*, 2011; Bertuol-Garcia *et al.*, 2018; Hoffmann, 2022; Haelewaters *et al.*, 2024).

To offset consequences of these shortfalls, numerous biodiversity knowledge gaps have been formally identified and described (e.g., Hortal*et al.*, 2015; Cottee-Jones *et al.*, 2016; Lees *et al.*, 2020; Martin *et al.*, 2023a, 2023b; Haelewaters *et al.*, 2024). Among relatively well-studied groups, including birds and other vertebrate groups (Hawksworth and Bull 2007), progress towards addressing these shortfalls has led to positive conservation outcomes (e.g., Lees *et al.*, 2020). However, addressing biological shortfalls is more easily achieved in well-studied, "emblematic" organismal groups, given these groups are frequently observed, collected, and monitored through space and time (Gauthier *et al.*, 2007; Mekonen, 2017), and are often identifiable in the field without requiring the examination of specimens (Haelewaters *et al.*, 2024). In contrast, understudied organismal groups are often characterized by extremely substantial knowledge shortfalls (Hochkirch*et al.*, 2021; Haelewaters *et al.*, 2024).

Poorly studied organismal groups, by definition, typically suffer from a lack of fundamental knowledge regarding their diversity and ecological patterns. There are several reasons why such groups exist. First, the biology of some organisms is intrinsically challenging to study due to their minute or microscopic nature, lifestyles (e.g., obligatory associations with other kingdoms), and habitats (e.g., soil, living tissues); these require adapted or newly developed (and often expensive) methodologies in order to study effectively (Schlick-Steiner *et al.*, 2010; Fišer *et al.*, 2018; Geisen *et al.*, 2019). Second, the visual appearance of some organisms conflicts with "beauty" criteria, making them less "appealing" for funding institutions and thus less targeted by conservation efforts. Well-studied and charismatic species are the most likely to receive conservation attention, even though many species in need of conservation efforts are found within understudied taxa (Sitas *et al.*, 2008; Small, 2011). Third, poorly studied taxa are in need of robust taxonomic expertise but at the same time are associated with a lack of taxonomists (Brewer *et al.*, 2012; Hochkirch *et al.*, 2022; Haelewaters*et al.*, 2024). As a consequence, the nature and scale of conservation shortfalls differ between well-known groups, such as birds and mammals, and understudied groups, which are mostly microbes and non-vertebrate animals (Parker, 2010; Anthony *et al.*, 2023).

Knowledge shortfalls due to sampling bias of certain vertebrate groups have been narrowed in recent years due to abundant expertise and increasing interest in citizen science (e.g., La Sorte and Somveille, 2020; Neate-Clegg *et al.*, 2020). However, these recent advances have not been observed for many understudied groups, leading to diverging conservation shortfalls. Recently, Laboulbeniomycetes (phylum Ascomycota), a class of minute fungi obligately associated with arthropods either for dispersal or as epibionts (**Figs. 1, 2**), has been proposed as a model system to illustrate the interplay between knowledge shortfalls and conservation in understudied taxa (Haelewaters *et al.*, 2024). The reasons for severe knowledge shortfalls in Laboulbeniomycetes are multifold, being linked to challenges related to estimating the number of species, geographical distributions, the identification and description of species, ecological and evolutionary inferences, and available methods and resources for the study of host–parasite interactions.

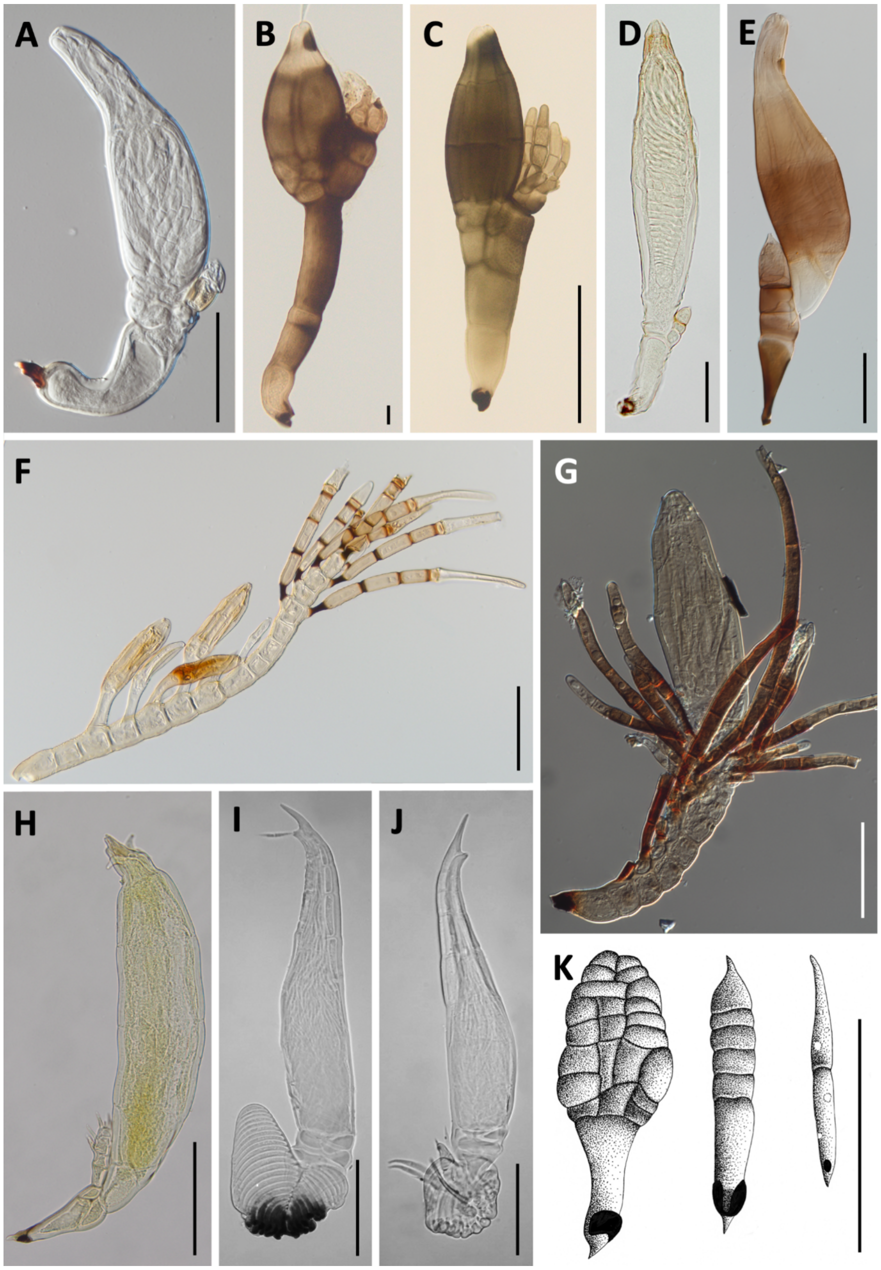

Figure 1: **Laboulbeniomycetes microfungi, including Laboulbeniales (A–H), Herpomycetales (I–J), and Pyxidiophorales (K).** **A**. *Gloeandromyces diversiformis* f. *musiformis*, recently described from tropical American bat flies (Van Caenegem *et al.*, 2023a). **B**. *Laboulbenia trogacti.* **C**. *Laboulbenia fuliginosa.* **D**. *Nycteromyces streblidinus.* **E**. *Neohaplomyces gusarovii.* **F**. *Enarthromyces indicus.* **G**. *Rhachomyces anophthalmi.* **H**. *Hesperomyces harmoniae*, obligatorily associated with the globally invasive ladybird *Harmonia axyridis* (Haelewaters *et al.*, 2022c). **I**. *Herpomyces stylopygae.* **J**. *Herpomyces shelfordellae.* **K**. *Thaxteriola* sp. Scale bars: **A, D, E, G, I**–**K** 50 µm; **B** 10 µm; **C, F, H** 100 µm. Photos: **A**–**E**, **G**–**J** Danny Haelewaters; **F** Ondřej Koukol. Drawings: Jingyu Liu.

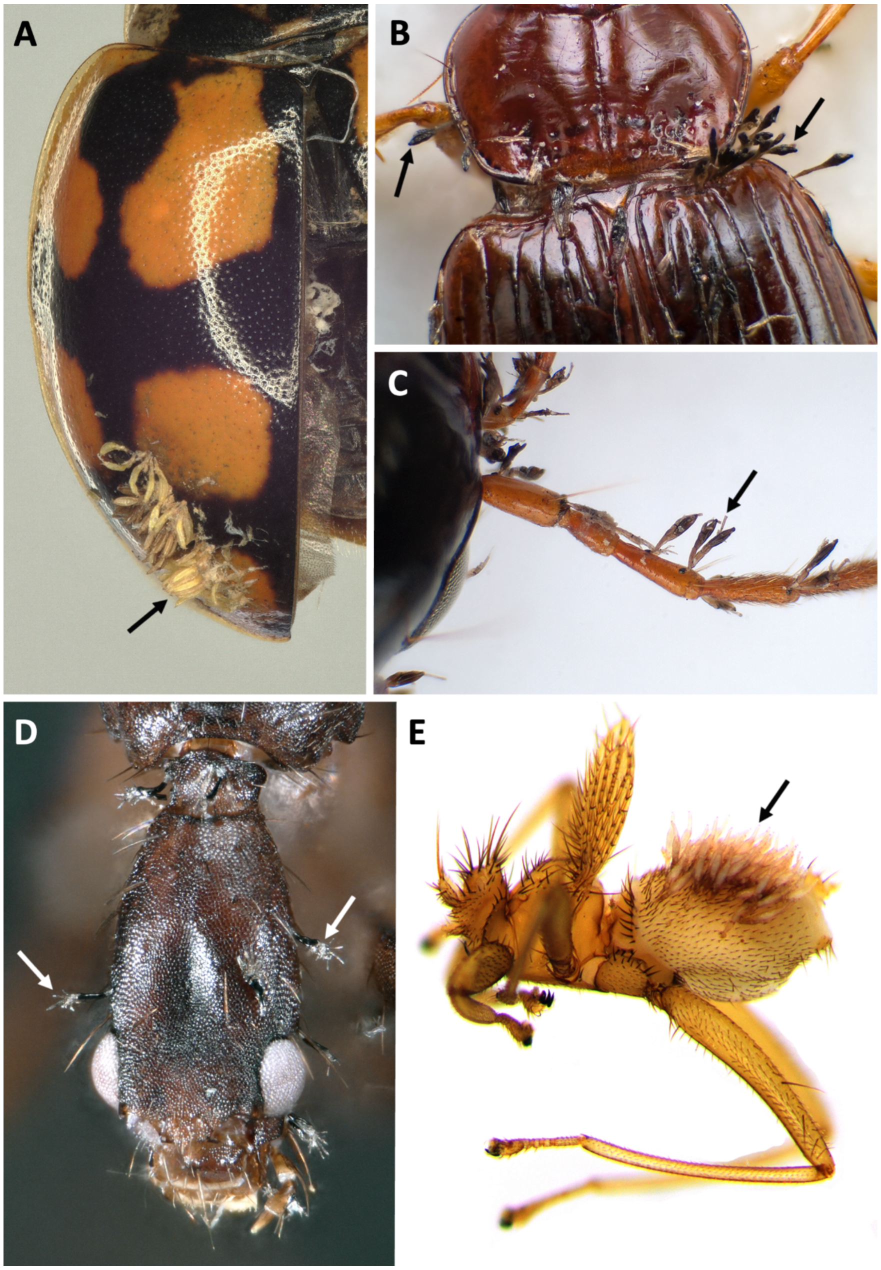

Figure 2: **In-situ photos of thalli of Laboulbeniales on the integument of their hosts.** **A**. *Adalia decempunctata* (Coccinellidae, Coleoptera) with *Hesperomyces* sp. nov. **B**. *Bradycellus harpalinus* (Carabidae, Coleoptera) with *Laboulbenia eubradycelli*. **C**. *Calathus melanocephalus*(Carabidae, Coleoptera) with *Laboulbenia calathi*. **D**. *Ecitophya gracillima* (Staphylinidae, Coleoptera) with *Laboulbenia ecitonis*. **E**.*Megistopoda proxima* complex (Hippoboscidae, Diptera) with *Gloeandromyces nycteribiidarum*. Photos: **A** Jerzy Romanowski, **B–C** Bart Horvers, **D** Danny Haelewaters, **E** Walter Pfliegler.

Laboulbeniomycetes is global in distribution with 2,478 described species (but with many more estimated to exist) unevenly distributed in three described orders (Laboulbeniales, Herpomycetales, Pyxidiophorales) and two unnamed clades (*Chantransiopsis*, *Laboulbeniopsis*) (Haelewaters *et al.*, 2019b, 2021a, 2024). Many species-level taxa with multiple host species and near-global distribution are hypothesized to be complexes of multiple, cryptic or near-cryptic species (Haelewaters *et al.*, 2018a). At the other end of the spectrum, recent work has revealed phenotypic plasticity in the class—with some phylogenetic species having multiple morphotypes (Haelewaters and Pfister, 2019; Van Caenegem *et al.*, 2023a). The study of Laboulbeniomycetes is also hindered by a historical and current lack of taxonomists which makes it difficult to distinguish true rarity from geographic biases related to sampling efforts. Specificity patterns are frequently observed in the group, with species often being restricted to a host, to a body position on the host, or to another microhabitat. Notwithstanding recent exceptions (Santamaria *et al.*, 2020; Perreau *et al.*, 2021; de Groot *et al.*, 2024), Laboulbeniomycetes have been studied using traditional tools and methods, while many other organismal groups have benefited from technological and methodological advances, such as machine learning and citizen science databasing (McKinley *et al.*, 2017; Wäldchen and Mäder, 2018; Tuia *et al.*, 2022).

This chapter aims to explore knowledge shortfalls that apply to the study of the Laboulbeniomycetes, as a model group of understudied organisms. Here, we address the different knowledge gaps that have been described for understudied organismal groups: Linnean, Wallacean, Prestonian, Darwinian, Raunkiaeran, Hutchinsonian, Eltonian (Hortal*et al.*, 2015), Parkerian (Lees *et al.*, 2020), Latimerian (Martin *et al* ., 2023a, 2023b), Scottian (Haelewaters *et al.*, 2024), and Ostromian shortfalls (Lopes-Lima *et al.*, 2021) (**Table 1**). In addition, we also introduce a new shortfall (Thaxterian), named after Roland Thaxter (1858–1932), professor at Harvard University and expert on Laboulbeniales, to address the lack of taxonomic expertise in a given organismal group. We also discuss the implication of each shortfall for the conservation of Laboulbeniomycetes and other understudied groups, as well as research avenues to fill such remaining gaps.

**Table 1. Main shortfalls of biodiversity knowledge, and their relevance to the study of Laboulbeniomycetes.**

| Shortfall | Aspect of knowledge | Definition |
|---|---|---|
| Linnean | Species diversity | Most species on the planet have not been described and catalog |
| Wallacean | Geographic distribution | Knowledge about the geographic distribution of most species is |
| Prestonian | Populations | Data on species abundance and population dynamics in space |
| Darwinian | Evolution | Lack of knowledge about the tree of life and the evolution of sp |
| Raunkiaeran | Functional traits and ecological functions | Lack of knowledge about species' traits and their ecological fun |
| Hutchinsonian | Responses to abiotic stresses | Lack of knowledge about the responses and tolerances of specie |
| Eltonian | Ecological interactions | Lack of knowledge on species' interactions and these interactio |
| Parkerian | Natural history knowledge | Lack of basic natural history knowledge |
| Latimerian | Species persistence | The number of species that are not known with certainty to be |
| Scottian | Species conservation assessments | Gap between the number of species assessed by the IUCN Red |
| Ostromian | Conservation and policy | Lack of conservation, methods, legal policy, funding, and aware |
| Thaxterian | Expertise | Lack of taxonomic expertise in an organismal group |

# Linnean shortfall

The order Laboulbeniales comprises 2,394 known species across 145 genera (Haelewaters *et al* ., 2024). Extrapolations from host utilization patterns derived from screening of beetles in Sulawesi suggest that the true number of Laboulbeniales species could range from anywhere between 5,000 to 75,000 (Weir and Hammond, 1997). If these estimates hold true, anywhere between 3% and 47% of Laboulbeniales species have currently been described. This issue is made more complex due to the presence of cryptic species complexes – which inevitably hampers taxonomic understanding of this order.

The order Herpomycetales encompasses 27 species in a single genus (Santamaria and Pedersen, 2021) and, in contrast to Laboulbeniales, has not undergone such a remarkable radiation, resulting in a less diversified clade that associates exclusively with cockroaches (Haelewaters *et al.*, 2019b). The current understanding of

Herpomycetales species diversity primarily stems from descriptions made between 1902 and 1931 except for two recently described species (Haelewaters *et al.*, 2019b, 2021c; Gutierrez *et al.*, 2020).

The order Pyxidiophorales includes 48 species in 12 genera (Haelewaters*et al.*, 2024). The classification of this order is particularly challenging due to the complex life cycles of its members, which typically exhibit three different morphs (Haelewaters *et al.*, 2021c). Unlike Laboulbeniales that mainly reproduce sexually, diverse groups of anamorphs are found within Pyxidiophorales (Schoch *et al.*, 2009). Therefore, estimating species diversity within this order is extremely difficult with the current state of knowledge, as multiple names have been attributed to different morphs. However, Haelewaters *et al.* (2021c) noted that GenBank contains environmental sequences that share >95% identity with known sequences of Pyxidiophorales. This suggests that the DNA of Pyxidiophorales species could be detected in environmental samples (Gorczak, 2023), and such molecular information may represent a promising, yet untapped, avenue to address knowledge gaps in species diversity within this order.

What is currently known of Laboulbeniomycetes species diversity is largely based on morphology. This understanding is biased due to the presence of species complexes (see Jörger and Schrödl, 2013), which obscures our comprehension of the true extent of the unknown diversity. Furthermore, the species accumulation curve for Laboulbeniomycetes features false plateaus, is non-monotonic, and fails to reach an asymptote. An important issue in estimating the extent of the Linnean shortfall for understudied organismal groups is a phenomenon referred to as the 'skewed specialist effect', whereby species accumulation curves are confounded by highly uneven species description rates due to the oversized efforts of a few taxonomists (Haelewaters *et al.*, 2024). Given the number of experts with a taxonomic interest in this group, uncertainties regarding the Linnean shortfall and its estimations will persist. These difficulties are further exacerbated by the fact that the only method to estimate the Linnean shortfall within Laboulbeniomycetes is through species discovery rates.

# Wallacean shortfall

The distribution of Laboulbeniomycetes is inherently tied to their arthropod hosts. As a result, the potential geographical range of an overlooked Laboulbeniomycetes species can be hypothesized to depend on the distribution of its hosts (e.g., *Troglomyces twitteri*; Santamaria *et al.*, 2020). However, the currently observed geographical distributions of Laboulbeniomycetes species generally do not coincide with the known distribution range of their hosts, underscoring the presence of a significant Wallacean shortfall for this class.

Many Laboulbeniomycetes species display patchy and fragmented geographical distributions, with most known from only one or a few localities (Haelewaters *et al.*, 2024). Known distributions of Laboulbeniomycetes vary considerably from one country to another. For instance, neighboring countries may differ substantially in the number of recorded species, as illustrated by the contrast between the USA—which hosts the highest reported diversity of the class—and Canada, which has few reported species (**Fig. 3**). The geographical distribution of Laboulbeniomycetes species is suggested to reflect the presence of or study areas of specialists rather than representing the 'true' distribution.

With increased sampling effort, Laboulbeniomycetes species with known restricted geographic distribution or that are associated with a limited host range may prove to be more widespread and occur on a broader host range than previously thought. Conversely, even the distribution of ubiquitous and well-known taxa may be biased, as their distribution may reflect the combined distributions of closely-related but distinct species that have been incorrectly grouped under the same name, e.g., *Laboulbenia flagellata* (Haelewaters *et al.*, 2019a) and *Hesperomyces virescens*(Haelewaters *et al.*, 2018a; Van Caenegem *et al.*, 2023b) species complexes. Furthermore, misidentifications arising from confusions between morphologically similar species (e.g., *Laboulbenia pseudomasei* and *L. pterostichi*, or *Monoicomyces britannicus* and *M. homalotae*; Santamaria and Pedersen, 2021), make it challenging to determine the true geographical distribution of certain Laboulbeniomycetes taxa.

Spatial records for this class are confined to online sources, which includes species-specific localities in species description and new records papers, specific data published in ecological studies (e.g., a Carabidae dataset; Pozsgai *et al.*, 2021), collaborative, collection-based (e.g., MyCoPortal) and citizen-based platforms (e.g., iNaturalist), and eDNA sequences in online molecular repositories (e.g., NCBI GenBank, UNITE). However, these data have not been systematically organized or mapped, leaving most countries and localities overlooked for Laboulbeniomycetes.

Fungal DNA in environmental samples (eDNA) is becoming increasingly common in diversity-based studies to map the geographical distribution of fungal taxa and ecological guilds (Tedersoo *et al.*, 2014). Publicly available eDNA data suggest that Pyxidiophorales are more ubiquitous than previously expected (Gorczak, 2023). However, only 17 'uncultured' sequences attributed to Laboulbeniomycetes are publicly available on the NCBI platform. These sequences represent 0.002% of the 1,074,404 'uncultured' sequences attributed to fungi (accessed 16th May 2024). Moreover, these 'uncultured Laboulbeniomycetes' sequences show high nucleotide similarity with numerous 'uncultured fungi' sequences, suggesting that many environmental sequences belonging to Laboulbeniomycetes are present in the NCBI platform but remain unnamed. Although, biases within commonly employed methods likely contribute to the lack of Laboulbeniomycetes sequences in eDNA datasets. Until more molecular-based taxonomic works on the Laboulbeniomycetes are accumulated, most of these environmental sequences will remain difficult to accurately identify, thus contributing to both Linnaean and Wallacean shortfalls.

Museum, institutional, and historical entomological collections have already demonstrated their potential as a significant reservoir of untapped morphological, molecular, and geographic diversity of Laboulbeniomycetes. New species have been formally described, and new country records have been made based on material from collections (Santamaria *et al.*, 2016; Haelewaters and Rossi, 2017).

Given the taxonomic and geographic diversity of arthropod specimens stored in museum collections, screening these collections for thallus-forming Laboulbeniomycetes appears a promising means of reducing the Wallacean shortfall. However, no large-scale screening of this kind has been undertaken thus far. In MyCoPortal, Laboulbeniomycetes represents 0.5% (854 of 157,866) and 0.08% (7,953 of 9,827,706) of total taxa and observations recorded on the platform, respectively (accessed 15th May 2024). Nevertheless, compared to the compiled global dataset of Haelewaters *et al.* (2024), the geographical distribution of MyCoPortal records mirrors some spatial trends, namely sampling effort biases (**Fig. 3**). Based on published and unpublished works on Laboulbeniomycetes relying on entomological collections, we assume that there are still many specimens of these ectoparasites to be found therein, and that examination of these could help fill the discontiguous geographical distributions of many taxa.

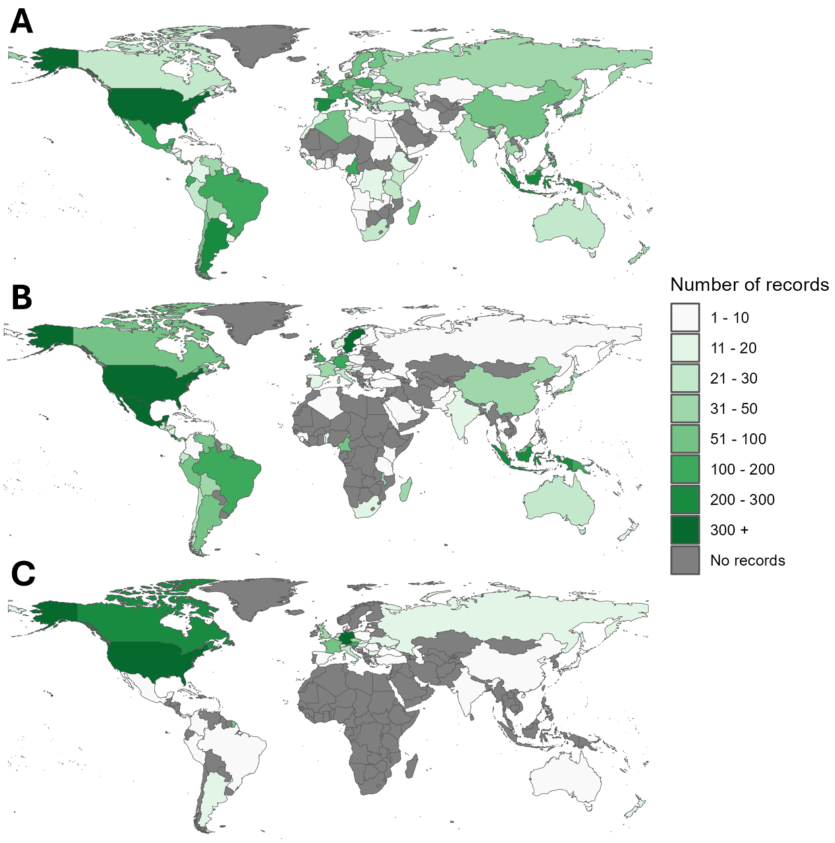

Figure 3: **Maps of the global distribution of Laboulbeniomycetes records. A.** Based on Haelewaters *et al.*'s (2024) dataset. **B.** Based on MyCoPortal records (n = 7777). **C.** Based on iNaturalist records (n = 3778). Grey corresponds to countries with no records. These maps indicate records per country and are therefore not informative of the precise spatial distribution of records within each country.

Citizen science is now recognized as a powerful tool for addressing biodiversity shortfalls, especially in undersampled regions, but its potential for Laboulbeniomycetes and other poorly-studied groups has yet to be fully explored. At first glance, it may seem that citizen science platforms are unlikely to be efficient in filling the Wallacean shortfall within the Laboulbeniomycetes. This is because their identification or even visualization is typically too complex for non-specialists, and as such citizen scientists generally do not upload records of Laboulbeniomycetes, which instead typically go unnoticed in the field. Hence, spatial records of Laboulbeniomycetes on citizen-based platforms like iNaturalist remain limited.

Among the 4,222 Laboulbeniomycetes records on iNaturalist, 99.6% are Laboulbeniales (as of 15 May 2024). Of these, 87% (3,642 observations) were assigned to *Hesperomyces harmoniae* (**Fig. 4**). This species, a parasite of the globally invasive ladybird *Harmonia axyridis*, has recently been used as a host-parasite model for broad-scale citizen science (de Groot *et al.*, 2024). Currently, Beetlehangers.org is the only large-scale, citizen-based online platform that collects and updates spatial records of a Laboulbeniomycetes species. A dataset of bat–bat fly–Laboulbeniales interactions is under construction (de Groot *et al.*, 2020), and Haelewaters *et al.* (2024) have created a global dataset of all known Laboulbeniomycetes species and their geographic records based on literature, MyCoPortal, and iNaturalist. However, despite these efforts, many countries completely lack iNaturalist records of Laboulbeniomycetes, and heavy sampling bias is evident (**Fig. 3**). This bias is also unsurprisingly reflected in the geographical distribution of iNaturalist records of *He. harmoniae* (**Fig. 4**).

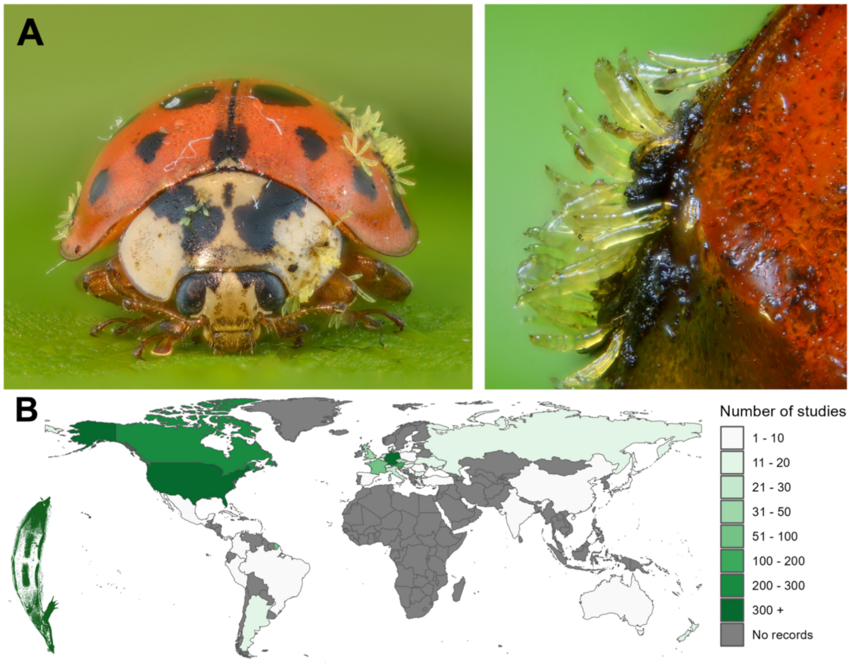

Figure 4: **iNaturalist photographs of *Hesperomyces harmoniae* on *Harmonia axyridis*.** Credits: Gilles Saint Martin. **B**. Choropleth map of the global distribution of *He. harmoniae* according to iNaturalist records, from de Groot *et al.* (2024). Drawing of *He. harmoniae* is based on a microscopic picture from Björn Sothmann's iNaturalist observation (#82052124).

The recent initiatives described above and the availability of online spatial records of select Laboulbeniomycetes offer promising pathways towards centralizing spatial records and underscore the importance of integrating complementary data sources to address the Wallacean shortfall for the Laboulbeniomycetes. Filling gaps in the Linnean shortfall is a prerequisite for enabling less common and more difficult-to-observe Laboulbeniomycetes species than *He. harmoniae* to be the focus of future initiatives specifically addressing the Wallacean shortfall. Increasing sampling efforts through the means mentioned above will be crucial to determine whether the patchy spatial distribution of most Laboulbeniomycetes species is merely a reflection of the distribution of researchers and citizen scientists, or if it can also be explained by biotic and abiotic environmental factors.

## Prestonian shortfall

Research on Laboulbeniomycetes in relation to the Prestonian shortfall (i.e., the lack of data on species abundance and population dynamics) has only been conducted in the context of parasite prevalence, defined as the number of infected host specimens in a given population (Haelewaters *et al.*, 2021c). These studies have focused on a limited number of parasite-host systems, including two “model” species for the order Laboulbeniales: *He. harmoniae* on *Ha. axyridis* and *Rickia wasmannii* on *Myrmica* ants. What stands out from these studies is that most Laboulbeniales species generally exhibit low prevalence on their hosts in natural populations, in contrast to the infection rates observed for Herpomycetales (**Table 2**). For Pyxidiophorales, prevalence data are currently absent in the literature. Given their microscopic nature and the fact that they cannot be cultured without their hosts in laboratory conditions, the low prevalence of Laboulbeniales on their hosts presents a limitation for addressing the Prestonian shortfall. Any study targeting this order must undertake significantly greater sampling efforts compared to other fungal, plant and animal species that occur more frequently on their substrate or habitats.

**Table 2. Overall parasite prevalence observed in Laboulbeniales and Herpomycetales (Pyxidiophorales are excluded lacking prevalence data).** Here, we define parasite prevalence as the number of infected host specimens in a given population (Haelewaters *et al.*, 2021c). The list is not intended to be exhaustive, nor to focus on environmental, seasonal and sexuality patterns (e.g., differential prevalence between habitats, seasons or host gender).

| **Prevalence (%)** | **Location** |
|---|---|
| **Herpomycetales** | |
| 100 | USA (Minnesota) |
| 96.8 | USA (Harvard University) |
| 8.77 to 86.36 | Hungary (pet stores) North America (biological supply company) USA (online pet store) |
| **Laboulbeniales** | |
| 1.1 | Canary islands |
| 9 | Europe (Albania, Croatia, Hungary, Italy, Portugal, Slovakia, Spain, Switzerland) |
| 3 | Central Europe (Hungary, Romania) |
| 4.6 | North and Central America (Costa Rica, Honduras, Mexico, Nicaragua, Panama) South America (Ec |
| from 2.3 to 3.8 | Portugal |
| 6.13 | Southeastern Europe (Bulgaria, Romania) |
| 0.6 | Indonesia (Sulawesi) |
| 1 | Finland and adjacent parts of former U.S.S.R. |
| 0 to 46.4, mean 17.9 | Central Europe (Croatia, Czech Republic, Germany, Hungary, Poland, Slovakia, Switzerland) |
| 0 to 100 | France |
| 0.2 | Netherlands |
| 19.5 | Belgium |
| 0.55 to 38 | Netherlands |
| 0 to 54.7 | United Kingdom |
| 0 to 100, mean 7.86 | Malaysia, Sulawesi, australia, Solomon islands |
| 0.6 | Brazil |

The reported prevalence of Laboulbeniales can vary greatly among species and host populations, as well as between sampling methods and observation scales. For example, Ceryngier *et al.* (2024) investigated the parasitism of ladybirds (Coccinellidae) by *Hesperomyces* and reported variations in parasite prevalence among the 10 infected host species and at the species level (e.g., *Hesperomyces*ex *St. tenerifensis*). Within the same locality in the Netherlands, two different sampling methods, namely pitfall trapping and direct sampling in nests, yielded different prevalence of *R. wasmannii*on their respective hosts (Haelewaters and De Kesel, 2020). Moreover, the prevalence of *He. harmoniae* on *Ha. axyridis* can be locally very high (Haelewaters *et al.*, 2021a).

To our knowledge, no research specifically addressing the abundance of Laboulbeniomycetes—in the sense of the number of fungal ectoparasites divided by the number of screened hosts (e.g., Ohanu *et al.*, 2024)—has been published to date (at either local or global scales). The data on parasite prevalence that have been gathered in the literature for a limited number of Laboulbeniomycetes taxa can be used to inform ecological traits (e.g., infection rates), although not to infer true abundance. At a global scale, some proxies of parasite prevalence have been provided in recent studies, such as with*Herpomyces* at the level of a single host (Wang *et al.*, 2016). Moreover, the Beetlehangers.org initiative used a definition of a record as "an observation of one host individual of *Ha. axyridis* that is infected with *He. harmoniae*, irrespective of the number of thalli" (de

Groot *et al.*, 2024). Since it is not considered with respect to the number of infected hosts and ectoparasite thalli, these large-scale data may provide an indication of prevalence for this specific taxon at global scale, but not true prevalence nor abundance.

Recent studies using eDNA metabarcoding techniques have detected Pyxidiophorales sequences in environmental samples and derived relative abundance of associated OTUs/ASVs (Tedersoo *et al.*, 2014; Haelewaters *et al.*, 2021c; Chaverri and Chaverri, 2022). Although the study of Laboulbeniomycetes through eDNA is still in its infancy, eDNA provides preliminary insights into the occurrence (presence/absence) and relative abundance (%) patterns of Laboulbeniomycetes in various soil environmental conditions and treatments. However, eDNA-based taxon abundance estimates are subject to multiple biases. Firstly, abundance measures in eDNA metabarcoding studies are known to be intrinsically biased, either from a biological or technical perspective (Fonseca, 2018; Nichols *et al.*, 2018; Lamb *et al.*, 2019). Secondly, metabarcoding studies derive relative estimates of abundance of taxa, i.e., the mean percentage of a given OTU/ASV in a given sample relative to all the other OTUs/ASVs, not absolute abundance (Roche and Mukherjee, 2022). Thirdly, relative abundance data calculated with high-throughput DNA sequencing techniques are semi-quantitative (Castaño *et al.*, 2020). Even if specific data transformations can account for the semi-quantitative nature of such studies (Tedersoo *et al.*, 2019), the quantitative performance of metabarcoding studies remains limited, with sequence reads being weak predictors of true taxa biomass in environmental samples (Lamb *et al.*, 2019). Therefore, relative abundance estimates of Laboulbeniomycetes (and in particular Pyxidiophorales), should be handled with caution and not considered as reflecting their true abundance. The important question of "*how eDNA data of Laboulbeniomycetes can help fill the Prestonian shortfall?* " should be tackled specifically in the light of recent methodological advances and initiatives towards quantitative metabarcoding frameworks (e.g., Shelton *et al.*, 2023).

Abundance, in conjunction with other population-level patterns such as geographic range, is essential for determining the Red List category of species according to the IUCN criteria (Rodrigues *et al.*, 2006; Maes *et al.*, 2015). However, the application of IUCN criteria and associated key concepts to fungi, including aspects such as mature individuals, population size, and generation length, presents a challenge (Dahlberg and Mueller, 2011). Prevalence data for thallus-forming Laboulbeniomycetes and eDNA-based relative abundances for Pyxidiophorales hinder mycologists from accurately estimating the number of individuals in natural populations and assessing population-level patterns for the application of IUCN Red List criteria. Consequently, most, if not all, Laboulbeniomycetes species lack sufficient data to be assessed in this regard. We urge the scientific community to discuss the extent to which current data on the population ecology of understudied organismal groups are applicable for red-listing and how they can be adapted to Laboulbeniomycetes. We also advocate for future research avenues focusing on Laboulbeniomycetes species abundance and population spatiotemporal dynamics in order to reduce the Prestonian shortfall.

## Darwinian shortfall

A baseline understanding of the evolutionary history of organismal groups, which includes knowledge about phylogenetic relationships between taxa and the origins of lineage diversity, is of great importance for conservation biology (Hartmann and André, 2012; Soares *et al.*, 2023). For instance, there are arguments that more evolutionarily distinct lineages should be prioritized for conservation (Isaac *et al.*, 2007). Some organismal groups possess nearly complete phylogenies, such as birds (e.g., Jetz *et al.*, 2012; Jarvis *et al.*, 2014; Prum *et al.*, 2015) and flowering plants (Guo *et al.*, 2023). For example, Zuntini *et al.* (2024) recently produced a groundbreaking phylogenomic tree of life encompassing more than half of known angiosperm genera.

Recent advances in molecular systematics and classification have drastically changed our vision of the fungal tree of life. Many authors have attempted to establish a complete and well-corroborated phylogenetic classification for the whole fungal kingdom (e.g., Li *et al.*, 2021), but this task has proven complex due to the considerable morphological, ecological, and genetic diversity of fungi (McLaughlin *et al.*, 2009). The fact that only a fraction of the estimated fungal diversity has been described is a massive detriment to the Darwinian shortfall. Phylogenetic trees based on single or multiple molecular markers have been, and continue to be, important in this regard. However, the information contained at the whole-genome scale is even more crucial for resolving deep nodes in the fungal tree of life and inferring new evolutionary relationships (Choi and Kim, 2017; Spatafora *et al.*, 2017; James *et al.*, 2020). Furthermore, fungal organisms only known from eDNA ('dark taxa'), and those that cannot be cultured, present further challenges towards resolving the fungal tree of life (Jones *et al.*, 2011; Tedersoo *et al.*, 2017). The evolutionary history of certain fungal groups is much better understood than others, with heavily understudied lineages such as Laboulbeniomycetes having a larger Darwinian shortfall.

The Laboulbeniomycetes tree of life is currently non-existent. Goldmann and Weir (2018) constructed a preliminary molecular phylogeny based on the conserved SSU rDNA gene. They specifically demonstrated the monophyly of the Laboulbeniomycetes and confirmed its relationship with the Sordariomycetes. At that time, two orders were recognized: Laboulbeniales and Pyxidiophorales. Haelewaters *et al.* (2019b) introduced a third order, the Herpomycetales, erected from the Herpomycetinae suborder. The description of this new order was based on three-locus and six-locus phylogenies, with sampling across the phylum Ascomycota and including limited Laboulbeniomycetes sequences. Blackwell *et al.* (2020) published a phylogenetic tree based on SSU and LSU rDNA genes supporting the fact that the thallus-forming Laboulbeniomycetes (Laboulbeniales and Herpomycetales) do not form a monophyletic clade. Preliminary efforts tend to support the placement of Herpomycetales as sister to Laboulbeniales, but challenge the currently accepted sister relationship of Laboulbeniomycetes and Sordariomycetes (**Fig. 5**). To date, the three formally described orders (Herpomycetales, Laboulbeniales, Pyxidiophorales) are supported by both morphological and molecular data, while two clades supported by DNA (*Chantransiopsis* and *Laboulbeniopsis*) remain undescribed.

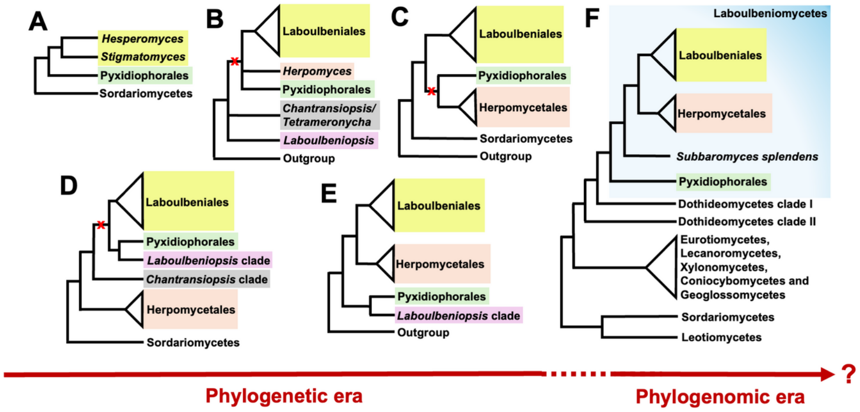

Figure 5: **Changes in evolutionary hypotheses within the class Laboulbeniomycetes over time. A**. Six-locus phylogeny based on 434 isolates, including four Laboulbeniomycetes isolates. **B**. SSU rDNA phylogeny based on 65 isolates. **C**. Three-locus rDNA phylogeny based on 61 isolates. **D**. Two-locus rDNA phylogeny based on 75 isolates. **E**. Three-locus phylogeny based on 130 isolates (modified from Law, 2024). **F**. Genome-based phylogeny relying on seven Laboulbeniomycetes genomes (modified from D. Haelewaters *et al.*, unpublished data). A to D, from Haelewaters *et al.* (2021c); red × indicating node without support.

Since the mid-1990s, understanding of the evolutionary relationships between clades of Laboulbeniomycetes has significantly improved with increasing taxon sampling and molecular data accumulation (Haelewaters *et al.*, 2021c). Despite these advances, the vast majority of nodes and phylogenetic relationships within Laboulbeniomycetes remain unresolved. Moreover, our understanding of the evolution of life history traits is also non-existent, as current molecular phylogenies only allow us to propose a few evolutionary hypotheses (e.g., thallus-forming forms, sexual and asexual reproduction, host specificity, haustoria presence), but not fully test or confirm them. To date, the molecular phylogeny of Goldmann and Weir (2018) remains the most complete for Laboulbeniomycetes.

A non-lacunary understanding of the Laboulbeniomycetes tree of life is hindered by multiple issues inherent to molecular sequencing. Molecular protocols for generating quality DNA sequences are challenging to apply for Laboulbeniomycetes. Thalli of many species of Laboulbeniales are heavily melanized, a trait reputed to reduce the success of DNA extraction and PCR amplification reactions (Haelewaters *et al.*, 2015b; Sundberg *et al.*, 2018). However, recent results from Van Caenegem and Haelewaters (2024) suggested that the melanin content in Laboulbeniales species is likely negligible, and the presence of melanin in thalli cells is therefore insufficient to explain the difficulties encountered with PCR and whole-genome amplification. Nevertheless, generating molecular data for Laboulbeniomycetes to study the evolution of species and life history traits is empirically challenging. This results in the majority of Laboulbeniomycetes species having never been sequenced, with only one draft genome having been generated for this class, namely for *Herpomyces periplanetae* (Haelewaters *et al.*, 2020b).

Although some molecular data have been generated for Laboulbeniomycetes species, there is a large locus and taxon sampling gap. The number of loci and sampled individuals per species are two key elements known to influence phylogenetic inference (Maddison and Knowles, 2006). The first molecular investigations of Laboulbeniales focused on the nrSSU given its convenience for priming compared to other markers (Haelewaters*et al.*, 2021a). Since then, several markers have been sequenced for Laboulbeniales species, including the nrLSU, ITS, *MCM7*, *TEF1*, and mtSSU. However, the number of sequenced loci for species of *Laboulbenia* remain very limited (Van Caenegem and Haelewaters, 2024). This loci sampling gap is generalizable to the whole Laboulbeniomycetes class. In other words, of the limited number of Laboulbeniomycetes species that have been sequenced, few are represented by more than one locus in public molecular databases. This is a serious challenge for reconstructing the Laboulbeniomycetes tree of life since sampling multiple loci increases species delimitation success and tree node resolution (Dupuis *et al.*, 2012).

Combining both dense gene and taxon sampling seems to hold great promise for resolving internal branches and unraveling new phylogenetic relationships within fungi (Li *et al.*, 2021). Due to the documented intragenomic variations in ribosomal DNA regions, including the widely used ITS region (Simon and Weiß, 2008; Paloi *et al.*, 2022; Bradshaw *et al.*, 2023), relying exclusively on it for fungal phylogenetic reconstructions may result in biased topologies. The low amplification success of most common markers for Laboulbeniomycetes has fostered the design of specific primers, including ITShespL and ITShespR specific to *Hesperomyces* and LabITS1 specific to Laboulbeniomycetes (Van Caenegem and Haelewaters, 2024). Despite this, loci that are informative at deeper nodes are still lacking for Laboulbeniomycetes.

The large taxon sampling problem is a serious limiting factor towards reaching a complete tree of life for the Laboulbeniomycetes since individuals are the basal unit from which DNA is extracted. This is confirmed by recent phylogenetic studies of the Laboulbeniomycetes where larger taxon sampling has resulted in novel evolutionary insights in the space of several years (Haelewaters *et al.*, 2021c). Large Laboulbeniomycetes taxon sampling remains challenging since Laboulbeniomycetes (1) are minute, frequently going unnoticed by both entomologists and mycologists, (2) are involved in obligatory associations, requiring the sampling of their host to detect them, (3) lack experts and resources to collect and study them across space and time, and (4) lack awareness within the scientific community and the general public, preventing them from being the focus of sampling campaigns. It is worth noting that this lack of large taxon sampling is fundamental behind all the shortfalls attributed to the Laboulbeniomycetes since knowledge acquisition cannot be achieved without having access to the material from which data are generated.

The first genome of a Laboulbeniomycetes species based on Illumina short-read sequencing marked a turning point in the study of their evolution. This so far uniquely publicly available 15-Mb draft genome assembly constitutes a reference for further genome-scale evolutionary analysis and functional genomic works for Laboulbeniomycetes (Haelewaters *et al.*, 2021a). An ongoing initiative to generate more Laboulbeniomycetes genomes demonstrates how genomic information challenges current knowledge that is based on multi-locus phylogenetic analyses (D. Haelewaters *et al.*, unpublished data). Furthermore, such data handled with genomic tools (e.g., gene prediction and annotation, comparative genomic analysis) could help answer questions related to (1) the molecular mechanisms behind host–interactions, (2) identifying specific genomic signatures of the ecological niches representative of the three Laboulbeniomycetes orders, and (3) the evolutionary origin of specific features of this class, such as the lack of hyphae. However, such research avenues require the acquisition of significantly more genomes from Laboulbeniomycetes species. Generating more genomic data will not only benefit the study of Laboulbeniomycetes evolution, but also ecological and evolutionary studies of other classes within Ascomycota and across the fungal kingdom generally, since genomes from understudied fungal groups are often lacking in whole-genome wide comparative studies. For instance, acquiring more genomes from Laboulbeniomycetes would benefit comparative genomics and phylogenomic investigations within Pezizomycotina (Melie *et al.*, 2023).

DNA of Laboulbeniomycetes retrieved from environmental sequencing could contribute to our understanding of the evolution of Laboulbeniomycetes, notably by unraveling still undescribed species and unknown lineages within Pyxidiophorales. However, as with other shortfalls, leveraging the potential of Laboulbeniomycetes eDNA to fill the Darwinian shortfall will require research efforts towards identifying eDNA corresponding to Laboulbeniomycetes species lost among 'uncultured' sequences in public repositories. Most fundamentally, this will necessitate building a solid, long-term, stable integrative taxonomic framework for Laboulbeniomycetes and enhancing discussion among the scientific community about the inclusion of eDNA sequences in taxonomy to fill the Darwinian shortfall in understudied organismal groups. In other words, Laboulbeniomycetes eDNA holds potential for eco-evolutionary studies only if the Linnean shortfall is more effectively reduced, otherwise the species represented by these eDNA sequences will remain undescribed and their ecology unknown.

The EDGE of Existence program has been a pioneering initiative towards phylogenetic conservation diversity and the prioritization of species conservation based on their evolutionary distinctiveness and threat status (Safi *et al.*, 2013). Despite recent advances for this program, such as discussions regarding EDGE metrics and the introduction of an EDGE2 protocol (Isaac and Pearse, 2018; Gumbs *et al.*, 2023), EDGE lists only exist for members of Fauna and Flora (specifically, amphibians, birds, corals, mammals, reptiles, sharks and rays, and gymnosperms;`https://www.edgeofexistence.org/edge-list/`). To date, no EDGE list has been created for Laboulbeniomycetes due to this Darwinian shortfall, nor indeed for any Funga (Nic Lughadha *et al.*, 2020). Notably, an already established fungal tree of life based on molecular systematics and phylogenomics could be used as a baseline for an EDGE list for fungi. Since Laboulbeniomycetes appear to be a suitable understudied group for an EDGE-based conservation approach, we call for increased momentum towards the acquisition of a substantially higher amount of genetic and genomic data for Laboulbeniomycetes and other understudied organisms to integrate this information to benefit their conservation.

## Raunkiaeran shortfall

Trait-based approaches are gaining increasing popularity in research that addresses ecological and evolutionary issues. Functional traits provide information about organismal performance, as well as the effects of organisms on ecological and ecosystem processes (Hortal *et al.*, 2015), and the ability of organisms to respond to global environmental change (McGill *et al.*, 2006; Kearney *et al.*, 2010). Functional trait databases for both animals and plants do exist and have proven valuable resources for conservation prioritization and understanding ecosystem functioning. For Fauna, examples include trait databases for birds (e.g., AVONET, Tobias *et al.*, 2022), cave-dwelling bats (e.g., DarkCideS, Tanalgo *et al.*, 2022), terrestrial animals (AnimalTraits; Herberstein *et al.*, 2022), mammals (PanTHERIA, Jones *et al.*, 2009), reptiles (Grimm *et al.*, 2014; Oskyrko *et al.*, 2024), ants (GlobalAnts, Parr *et al.*, 2016) and databases focused on specific lifestyles and geographical locations like European subterranean spiders (Mammola *et al.*, 2022) and tropical American frugivorous vertebrates (Frugivoria, Gerstner *et al.*, 2023). For Flora, examples include the widely used TRY dataset for plants (Kattge *et al.*, 2011, 2020) and other trait-based datasets publicly available for specific plant families and localities, such as worldwide Arecaceae (PalmTraits, Kissling *et al.*, 2019), pantropical Melastomataceae (MelastomaTRAITs, Reginato *et al.*, 2024), Euro-Mediterranean trees (WOODIV, Monnet *et al.*, 2021), northwestern European flora (Kleyer *et al.*, 2008), Chilean woody plants (Rasgos-CL, Alfaro *et al.*, 2023), Chinese land plants (Wang *et al.*, 2018), Andean plants (FunAndes, Báez *et al.*, 2022), Mediterranean Basin plants (Tavşanoğlu and Pausas, 2018), and forest bryophytes (BryForTrait, Bernhardt-Römermann *et al.*, 2018). The analysis of such plant functional traits holds one of the greatest potentials to predict ecosystem services and underscores its relevance to human societies (Brown and Anand 2021).

Trait-based research for microbes is much less numerous and represents a relatively recent field compared to macroorganisms. Functional traits are more complex to measure for organisms that, unlike most animals and plants, are microscopic and that depict remarkable taxonomic and ecological diversity. Despite this, growing interest in microbial functional traits has emerged, with traits covering gene, organism, guild and community levels (Yang, 2021). Given the importance of microbes in terms of biomass and fundamental ecosystem functions, microbial trait research represents a promising avenue to increase our understanding of ecosystem-scale processes, and inform biological conservation and management (Bodelier, 2011). Moreover, due to the link between microbial traits and phylogeny (Martiny *et al.*, 2013, 2015), a microbial trait-based approach might be all the more suitable for an EDGE list approach, given that the Darwinian shortfall is first solved.

Several functional trait databases have been created for microorganisms, including for bacteria, e.g., BactoTraits (Cébron *et al.*, 2021), and fungi and fungus-like organisms, e.g., FUNGuild (Nguyen *et al.*, 2016), Fun$^{\text{Fun}}$ (Zanne *et al.*, 2020), and FungalTraits (Põlme *et al.*, 2020). Particularly for Funga, initiatives are also emerging towards a trait-based approach for macrofungi comprising both functional and non-functional traits relevant for management and conservation (Dawson *et al.*, 2019). Despite this, many fungal groups lack specific information about their traits and are not included in the latter databases. Therefore, trait databases for several understudied fungal groups, including Laboulbeniomycetes, remain non-existent.

Trait-based research for Laboulbeniomycetes is still in its infancy. Historically, trait information for Laboulbeniomycetes was morphological, being measured for purely taxonomic purposes. Nowadays, despite the increasing use of molecular tools in fungal taxonomy and systematics, morphological traits are still the foundation of the current classification system of Laboulbeniomycetes. Although they are limited in number, these morphological traits are primarily related to e.g., thalli, cells, appendages, antheridia, perithecium, and ascospores, and are compared to identify similarities and differences among related species. For example, the linear superposition of cells constitutes an informative morphological trait shared by Laboulbeniomycetes members and supported by rDNA (Henk *et al.*, 2003). These morphological traits may be potential candidates for functional traits; however, it is still unknown if these traits have a significant link to species survival.

Only very recently have researchers begun to pave the way for a functional trait-based approach for Laboulbeniomycetes. Haelewaters and De Kesel (2020) called for further research linking patterns of speciation to morphological and life history traits, introducing the haustorium as a promising candidate. Haelewaters *et al.* (2022b) applied the One-Host-One-Parasite model (1H1P) to haustorial thallus-forming Laboulbeniomycetes and hypothesized that the presence of haustoria governs host specificity, while species without haustoria are primarily influenced by microhabitats. Although this has not been formally tested, the haustorium should represent a good candidate for being a functional trait because it may inform about taxa fitness and survival as no thallus-forming Laboulbeniomyetes are known to survive without a living host (Haelewaters *et al.*, 2021a).

In parallel, ecological and functional studies on bats and bat flies, which are involved in tripartite interactions with Laboulbeniales (i.e., fungi parasitizing flies parasitizing bats), could serve as initial points for future trait-based approaches for Laboulbeniomycetes. These studies have employed the concept of ecomorphology and have focused on the interplay between bat functional traits and parasitism by bat flies (Haelewaters *et al.*, 2021b). de Groot *et al.* (2020) tested the hypothesis that parasitism by Laboulbeniales may be influenced by bat fly ecomorphology. However, they found no statistically significant results to support this hypothesis. To date, no studies have investigated the association between hyperparasite morphological traits and host ecomorphology, nor addressed broader questions for the class, such as whether Laboulbeniomycetes species can be grouped into ecomorphological types, or how environmental factors may influence Laboulbeniomycetes traits.

The ecological role of Laboulbeniomycetes traits remains, at best, unclear. However, there are several pieces of information in the literature that can guide future trait-based research for Laboulbeniomycetes, particularly with the aim of (1) establishing lists of morphological and life history traits applicable to Laboulbeniomycetes, for example, using the list of Llopis-Belenguer *et al.* (2019) as a reference, (2) addressing whether these traits, including morphological traits or certain variables linked to their life cycle (e.g., infection rate, position and host specificity, presence of a haustorium) can be considered as functional traits, (3) assessing the ecological implications of these traits, and (4) investigating how traits vary according to changing biotic and abiotic factors. For instance, for bat fly-associated Laboulbeniales, the factors driving morphological differences within phylogenetic species remain unknown (Van Caenegem *et al.*, 2023a). Haelewaters and Pfister (2019) demonstrated the existence of position-induced morphological plasticity and multiple morphotypes depending on the position on the host within phylogenetic species. Blackwell (1980) suggested that observed morphological variations could potentially be host-mediated. Dogonniuck *et al.* (2019) also proposed that intraspecific variations may result from growing on different positions of the host integument. Laboulbeniales (eco)morphotypes are likely the result of morphological adaptations induced by position-related stresses (e.g., nutrient availability). Moreover, among the specimens examined by Blackwell (1980), a slight tendency for longer thalli was observed for specimens occurring on the eastern part of their range. Longer thalli, which indicate more synthesized fungal biomass, can provide information about favorable conditions for their growth and can be related to individual survival. These are examples of hypotheses that could be tested in future trait-based Laboulbeniomycetes studies.

Fundamental morphological taxonomic work, in addition to studies focused on the interactions between Laboulbeniomycetes and other organisms, could drive the development of trait-based research; we encourage further investigation of such research avenues. Given the suggested potential of Laboulbeniales as indicators of ecosystem health (Kaishian, 2021), understanding key species traits and their ecological functions will be crucial for reducing the Raunkiaeran shortfall and building trait-based conservation approaches. However, due to the strong connection with the Linnean shortfall, significant advances in the field of taxonomy are essential for constructing a reliable ecological and functional trait-based approach for the Laboulbeniomycetes (Tedersoo *et al.*, 2018).

# Hutchinsonian shortfall

In the context of global change, understanding a species' response to shifting environmental conditions is crucial for devising realistic and adapted conservation strategies. The reduction in species' realized niche breadth represents one important explanation for the decline in individuals in natural populations (Scheele *et al.*, 2017). Despite inherent biases, the application of niche modeling strategies, in conjunction with future climatic scenarios, has proven to be particularly beneficial for predicting species habitat gains/losses and identifying conservation opportunities (Schwartz, 2012). Moreover, abiotic conditions are essential elements that define ecosystems and are among the scientific foundations for an IUCN Red List of ecosystems (Keith *et al.*, 2013; Rodríguez *et al.*, 2011). To incorporate species distribution and niche modeling approaches, as well as the abiotic dimension of environmental changes into conservation plans, baseline knowledge on the relationship between taxa presence/absence, abundance, and habitat abiotic conditions is required. However, this type of knowledge varies among organismal groups.

While the ecological niches of many animals and plants have been extensively studied, microorganisms have long been overlooked in this regard due to the inherent complexity of microbial systems and technological limitations (Malard and Guisan, 2023). Before the advent of molecular environmental tools, measuring the abiotic conditions in which a given microbial species or group preferentially occurs was particularly challenging given the "hidden" nature of microorganisms. In addition to challenges related to measuring abiotic parameters, microbes needed to be isolated through culturing methods, and for the rare species producing macroscopic structures, such as macrofungi, strong observational and taxonomic skills were required. However, most microbial species are unculturable and most fungal species do not produce macroscopic spore-bearing apparatus. Thus, with these 'traditional' methods, abiotic conditions were specifically assessed for only a small portion of the entire microbial diversity. This means many microorganisms have been overlooked with respect to their environmental tolerances.

High-throughput sequencing enabled the rediscovery of the environmental and habitat preferences of microorganisms (Malard and Guisan, 2023). Since then, studies investigating the relationships between eDNA-based microbial community metrics and abiotic factors are increasing in number, particularly for soil ecosystems where most microbial diversity is found (Anthony *et al.*, 2023). This has led to, for example, the publication of a global atlas of soil bacteria, which identified habitat preferences for dominant bacterial phylotypes (Delgado-Baquerizo *et al.*, 2018), as well as several major contributions towards understanding global fungal diversity distribution (Tedersoo *et al.*, 2014; Egidi *et al.*, 2019; Větrovský *et al.*, 2019). However, such global studies cannot be performed for understudied groups, such as Laboulbeniomycetes, due to their large Hutchinsonian shortfall.

Although biotic habitat conditions are crucial in host–parasitic interactions, abiotic environmental conditions controlling host distribution or the abiotic microhabitats on the hosts may also control parasite occurrence, and even parasite host specialization (Bellis *et al.*, 2021). Martins *et al.* (2021) reported the importance of climatic factors in explaining the global distribution of helminth parasites of amphibians. Vacher *et al.* (2008) also underscored the importance of integrating abiotic factors in exploring variations in plant fungal parasite richness. However, the distribution of many poorly known fungal parasites remains understudied, notably in the context of arthropod–parasite interactions.

Information regarding the environmental factors that influence Laboulbeniomycetes species is sparse. Such data exist for only a handful of species, with a bias towards parasites of invasive host species and thallus-forming Laboulbeniomycetes species. Similar to other fungal ectoparasites, it was initially thought that Laboulbeniales were solely, or primarily, influenced by the environmental conditions selected by the host. However, as postulated for *Laboulbenia slackensis* (De Kesel, 1996), since almost the entire part of the thallus (except for haustoria that penetrate the integument hosts in haustorial species) develops outside the integument of the host, abiotic environmental conditions should play a role in explaining the its presence and that of other Laboulbeniales traits. Indeed, since the late 20th century, researchers have accumulated evidence that the prevalence and development of Laboulbeniales are also largely influenced by abiotic factors.

De Kesel (1996) was among the first studies to demonstrate that the host was insufficient to explain the development of a Laboulbeniales species, *L. slackensis.* He showed that the relative growth of *L. slackensis* populations was affected by soil composition under which the host was reared, and that its optimal development conditions corresponded to the optimal habitat selected by the host. Since then, studies have focused on how infection rates respond to certain environmental conditions. For example, Welch *et al.* (2001) observed a higher parasite prevalence of *Hesperomyces virescens* sensu lato on the native ladybird (*Adalia bipunctata*) in London, with higher parasite prevalence being observed in urban areas. Szentivanyi *et al.* (2021) demonstrated that climatic factors could explain distribution patterns of *Arthrorhynchus* spp. on bat flies and *Rickia wasmannii*on *Myrmica* ants. The likelihood of observing Laboulbeniales infections was higher under low annual mean temperature and humidity. Gippet *et al.* (2021) also confirmed that environmental conditions could drive distribution patterns of Laboulbeniales, with *Laboulbenia formicarum*presence on invasive ant host associated with hotter and dryer climatic conditions in low elevation areas at the landscape scale—which contrasts with results from Szentivanyi *et al.* (2021). In accordance with Welch *et al.* (2001), Gippet *et al.* (2021) also found a positive effect of urbanization on *L. formicarum* prevalence. Contrasting results have also been obtained by Haelewaters *et al.* (2022a) where climate and landscape composition did not significantly affect infection probability of *He. virescens* on *Ha. axyridis.* de Groot *et al.* (2024) also showed that *He. harmoniae* was more recorded in areas under anthropogenic influence.

All these studies suggest that the response of Laboulbeniales species to abiotic factors might be species-dependent and linked to microclimatic factors. For instance, Péter *et al.* (2022) suggested that roost microclimatic conditions (higher humidity) might explain the higher infections of Laboulbeniales on bat flies in their study. In their discussion, de Groot *et al.* (2020) also noted that the distribution of Laboulbeniales is determined by both abiotic factors and host availability, which might partially explain why bat fly eco-morphotype did not significantly influence infection prevalence.

The limited number of studies that contributed to addressing the Hutchinsonian shortfall is almost exclusively focused on Laboulbeniales; we are not aware of any similar community ecology studies of Herpomycetales or Pyxidiophorales. However, for the latter, some community ecology studies using eDNA that, by chance, amplified Laboulbeniomycetes sequences in their environmental samples correlated their presence and abundance with abiotic variables. For example, Beriot *et al.* (2023) found that Pyxidiophorales were related to a high content of plastic in agricultural parcel soils from Spain. Wang *et al.* (2022) reported a positive correlation between Laboulbeniomycetes abundance and iron content. Li *et al.* (2023) showed Laboulbeniomycetes abundance was positively and negatively correlated with sand and phosphorus availability, respectively. Although these results are worth mentioning, they are opportunistic. Nevertheless, environmental sequencing might hold great promise to provide new insights into the ecological conditions controlling the distribution of the order Pyxidiophorales across space and time.

Biases towards parasites of invasive species may be explained by the fact that invasive hosts tend to be more abundant, which increases the chance of collection and, thus, observing parasites. Moreover, having a sufficient number of infected host specimens for a community ecology approach is a prerequisite for obtaining enough statistical power to correlate parasite traits with abiotic environmental factors. However, the habitat preferences of most Laboulbeniomycetes species remain unknown to date, leaving the question of "*how their distributions might change with global change and anthropogenic activities?* " unanswered.

This lack of knowledge hinders the integration of Laboulbeniomycetes into conservation and ecosystem management frameworks. A recent study suggested that the global network of protected areas does not adequately represent the environmental and habitat conditions of more than three-quarters of even the most well-studied organismal groups (Hanson *et al.*, 2020). In light of such observations, we can safely assume that current protected areas are even less suited to the ecological niches of groups as specialized and poorly known as the Laboulbeniomycetes, which further underscores the need to fill the gaps in Hutchinsonian knowledge. We encourage future research to consider, as a starting point, easily targeted and surveyed abiotic variables (e.g., relative humidity, precipitation, elevation, latitude, etc.), either through direct sensing or indirectly using climatic variable databases, as done by Szentivanyi *et al.* (2021), Gippet *et al.* (2021), and Haelewaters *et al.* (2022a). Putting efforts into reducing the Hutchinsonian shortfall for Laboulbeniomycetes, thus increasing our understanding of which abiotic factors affect their presence/absence, abundance, dispersal capacities and habitat colonization, could increase our ability to optimize their sampling and facilitate their integration in conservation plans.

# Eltonian shortfall

No one can pretend to understand biological systems without considering species interactions (McCann, 2007). Interactions are integral to community ecology studies, as they play pivotal roles in shaping species distributions and assemblages across spatial scales (Wisz *et al.*, 2013). Their study can also provide new insights into spatially and temporally larger ecological, biogeographical and evolutionary patterns (Wiens, 2011; Lawrence *et al.*, 2012). The complexity and diversity of biotic interactions have led researchers to view these interaction structures as networks (Delmas *et al.*, 2019). However, biotic relationships among species may face significant threats due to global change, making species responses increasingly challenging to predict in rapidly changing environments (Tylianakis *et al.*, 2008). Consequently, several initiatives have advocated for the integration of species interaction and associated networks into conservation and ecosystem management strategies (Tylianakis *et al.*, 2010; Heinen *et al.*, 2020).

The numerous types of species interactions involving animal and plant species have been extensively studied. For instance, predator-prey interactions in animal ecology and behavioral studies have been well documented and modeled, including their underlying processes and responses to environmental change (Chesson, 1978; Berryman, 1992; Abrams, 2000; Boyce, 2000; Beauchamp *et al.*, 2007; Brose *et al.*, 2008). For plants, mutualistic interactions with mycorrhizal fungi constitute one of the most important research fields in terrestrial ecosystems, particularly regarding forests and agricultural systems (Rillig, 2004; Johansson *et al.*, 2004; van der Heijden *et al.*, 2015). These ecologically and evolutionarily important interactions are known to drive key ecological processes and have major implications for human societies, conservation, and ecosystem responses to global change (Field *et al.*, 2020).

Fungi themselves engage in multiple interactions with other organismal groups, such as bacteria (Wargo and Hogan, 2006; Deveau *et al.*, 2018), mammals (Elliott *et al.*, 2022), birds (Elliott *et al.*, 2019), and invertebrates (Santamaria *et al.*, 2023), especially insects (Biedermann and Vega, 2020). Insect–fungal interactions, which are quite common and involve two of the most species-rich organismal groups on earth, are considered a significant part of the hidden, overlooked, and still undescribed fungal diversity (Blackwell and Vega, 2018). In particular, Laboulbeniomycetes has received considerably less attention regarding species interactions, including associated mechanisms, and the ecological, evolutionary, and conservation implications, compared to other organismal groups, even within the fungal kingdom.

Given their obligatory associations, studies have primarily focused on the interaction between fungal parasites and their hosts. The majority of Laboulbeniales species are biotrophically associated with host species belonging to Coleoptera, followed by Diptera. Herpomycetales are exclusively associated with cockroaches (Blattodea), and Pyxidiophorales mainly parasitize other fungi and interact with arthropods for dispersal (Haelewaters *et al.*, 2021a). The specific nature of the biotrophic interaction between Laboulbeniales and their hosts has always been a topic of interest for entomologists and mycologists. One line of investigation has been to determine if infections by Laboulbeniales have negative effects on their hosts. In this regard, the majority of knowledge gathered so far has focused on three Laboulbeniales species, including *He. virescens*sensu lato (*He. harmoniae* mostly), *Rickia wasmannii* and *Laboulbenia formicarum* (**Fig. 6**). In addition to being the most-well known fungal parasite of *Myrmica* ants in Europe (Witek *et al.*, 2014), *R. wasmannii* might be one of the most well-studied host–Laboulbeniales systems of the effects of fungal infection on the hosts. For example, fungal infections by *R. wasmannii* have documented effects on *Myrmica* hosts, including behavioral ones.

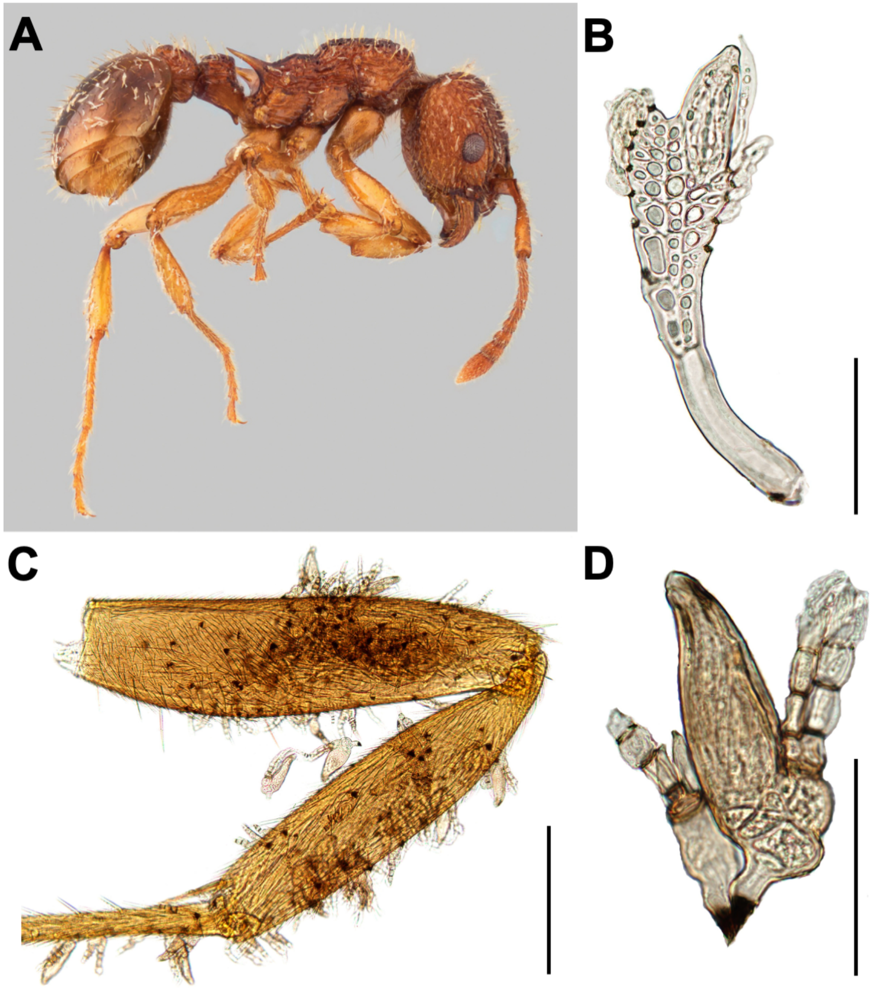

Figure 6: **Illustrations of *Rickia wasmannii* (A-B) and *Laboulbenia formicarum* (C-D).** **A**. *Myrmica sabuleti* (Formicidae, Hymenoptera) infected by *Rickia wasmannii*. **B**. *Rickia wasmannii* thallus. **C**. *Lasius neglectus* leg infected by *Laboulbenia formicarum*. **D**. *Laboulbenia formicarum* thallus. Scale bars: **B, D** 50 µm; **C** 200 µm. Photos: **A** Theodoor Heijerman, **B–D** Walter Pfliegler.

Although causality links have not always been established, fungal infections have been shown to be associated with lower lifespan and higher frequency of allogrooming (Csata *et al.*, 2014), higher sensitivity to water-deprivation (Báthori *et al.*, 2015; Csata *et al.*, 2017), reduced aggressivity and boldness (Báthori*et al.*, 2017), smaller body size (Csősz *et al.*, 2021), reduced cuticle thickness (Csata *et al.*, 2018), and increased immunity response (Orbán-Bakk *et al.*, 2024). For *He. harmoniae*, few studies suggest negative effects on the hosts (Haelewaters *et al.*, 2017b; Nedvěd *et al.*, 2023), although one study based on laboratory bioassays presented evidence for increased mortality (Haelewaters *et al.*, 2020a). For *L. formicarum*, Konrad *et al.* (2015) showed that fungal infection was associated with reduced survival of hosts under starvation, longer self-grooming, and elevated expression of immune-related genes. Nevertheless, there is still a large knowledge gap on the effects of Laboulbeniales infections on the fitness traits of their hosts since the effects of the vast majority of such infections remain unknown, and many fitness traits related to fertility, reproduction, and immune response remain unexplored, even for the aforementioned study cases.

Apart from their hosts, some studies have also reported interactions between Laboulbeniales and other organismal groups. For example, it has been observed that Laboulbeniales infection increased the survival of hosts infected by *Metarhizium brunneum*, suggesting an anti-pathogen effect (Konrad *et al.*, 2015). Other co-infections involving Laboulbeniales have been observed in the literature, such as with *Ha. axyridis* being infected by *He. harmoniae* and *Parasitylenchus bifurcatus*and either *Beauveria bassiana* or *Metarhizium brunneum* (de Groot and Haelewaters, 2022). However, the specific nature of the interactions between Laboulbeniales and other natural enemies of their hosts, as well as the associated mechanisms, necessitates further investigations, as emphasized for the recently recorded *Stigmatomyces majewskii–Drosophila suzukii* system (Yamazaki *et al.*, 2023). Furthermore, Lubbers *et al.* (2022) recently uncovered the presence of bacterial biofilms on three Laboulbeniales species—*Laboulbenia collae* on *Paranchus albipes*, *Laboulbenia flagellata* on *Limodromus assimilis*, and *He. virescens* sensu lato on *Ha. axyridis*—setting the stage for future research on the biotic interaction between Laboulbeniomycetes and their associated microbial communities.

All these studies suggest that the traditional view of host–Laboulbeniales associations, which were thought to involve only the ectoparasites and the infected host (i.e., bipartite), does not accurately reflect the true complexity of such systems. It is possible that certain host–parasite interactions hitherto considered or studied as bipartite systems may actually be multipartite (**Fig. 7**). This is particularly plausible given that Laboulbeniales are known to be part of hyperparasitic associations, including ones involving bats and bat flies (Haelewaters *et al.*, 2021b) as well as birds and feather lice (Eichler, 1942). Such obligate multitrophic interaction networks underscore the Eltonian shortfall for the Laboulbeniales order alone. The interactions between Laboulbeniales and bat flies remain understudied; however, in the context of the Eltonian shortfall, indirect interactions between bats and the parasites of their parasites also constitute an unexplored research area.

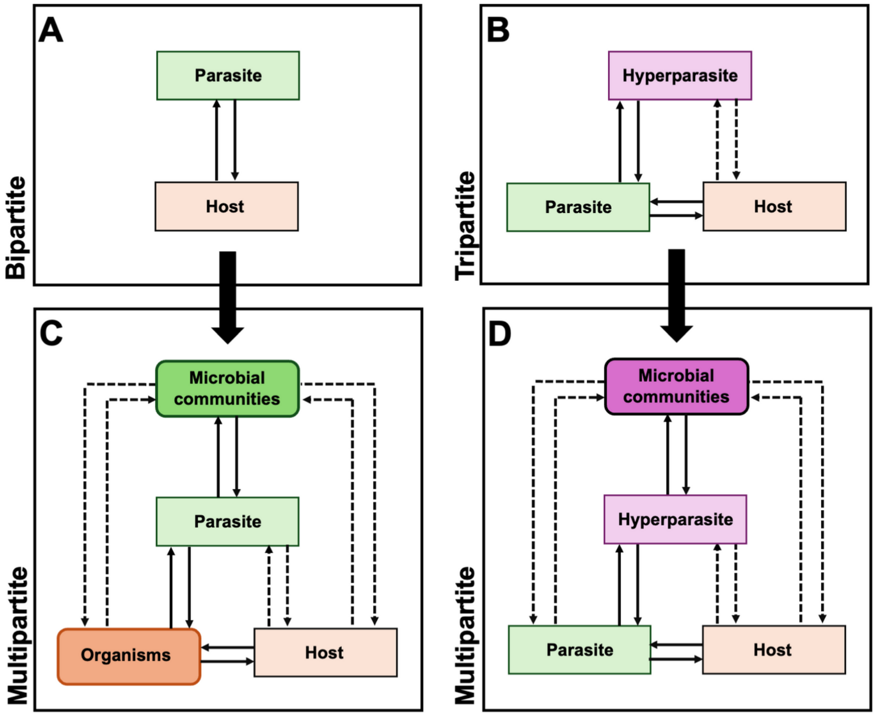

Figure 7: **Complexity of interactions involving Laboulbeniales and Herpomycetales.** The latter were known to be involved in bipartite (**A**) and tripartite interactions (**B**). Current literature indicates that the bipartite and tripartite systems are actually multipartite interaction networks (**C-D**). In **A**, 'parasite' refers to Laboulbeniales, while in **B**, fungal ectoparasites are referred to as hyperparasites. Full arrows indicate direct interactions, while dotted arrows indicate indirect interactions. Organisms encompass other interacting taxa or communities, such as parasites, pathogens, or microbial communities. Most of these interactions are still unknown to date. Illustration inspired by Bermúdez-Cova *et al.* (2024).

Although they have not been extensively studied, some potential interactions involving *Pyxidiophora* species have been reported. For instance, complex potential interactions have been proposed for the system comprising *Pyxidiophora* species, nematophagous and mycoparasitic fungi, bark beetles, and phoretic mites (Kirschner, 2003). Furthermore, based on eDNA, Chaverri and Chaverri (2022) suggested potential new interactions for dispersal between *Pyxidiophora* and the fig pollinating wasps *Pegoscapus* spp. and the bat *Ectophylla alba.* Given that Pyxidiophorales are also detected in environments as complex as soils, it is easy to imagine the extent of the Eltonian shortfall at the class level. Therefore, we particularly emphasize the need to leverage Laboulbeniomycetes eDNA in public repositories and metabarcoding-based ecological studies, as they can reveal a plethora of new biotic interactions. Consequently, Laboulbeniomycetes represent a suitable interaction system for network ecology; an approach we also advocate to handle the full complexity of these interactions.

In addition to documenting interactions between Laboulbeniomycetes and other species, it is important to decipher the mechanisms involved to understand both the ecological and evolutionary implications. One structural element directly involved in the interaction between the ectoparasite and the host is the haustorium. Haustorial structures are present in less than 10% of described Laboulbeniales taxa (13 of 145 genera), while all Herpomycetales species are haustorial (Haelewaters *et al.*, 2022b). This type of structure is therefore relatively rare within the Laboulbeniales. For example, Tragust *et al.* (2016) found no evidence of penetration structures for four of six ant-parasitizing Laboulbeniales—*L. formicarum* on *Lasius neglectus*, *Rickia wasmannii*on *Myrmica scabrinoides*, *Laboulbenia camponoti* on *Camponotus sylvaticus*, and *Rickia lenoi-*

*rii*on *Messor wasmannii*—using light microscopy and transmission electron microscopy. Rather, they are attached to the host using a hook-like foot structure that does not form penetration pores.

Using micro-computed tomography, Reboleira *et al.* (2021) also found no haustorial-like penetration structures in *Rickia gigas* on *Tropostreptus hamatus*, while they did observed a haustorium with sided branches penetrating the host cuticle in *Arthrorhynchus nycteribiae* on *Penicillidia conspicua*. Similar to Tragust*et al.* (2016), Haelewaters *et al.* (2022b) also illustrated the absence of penetration structures for *R. wasmannii*, while showing the presence of a penetration pore for *He. virescens*, using scanning electron micrography. High resolution micro-photographs of penetration structures are available for only a handful of Laboulbeniomycetes taxa, with histopathology studies being species-focused. These recent examples illustrate the substantial knowledge gap related to the mechanisms governing the interactions between haustorial and non-haustorial taxa and their hosts.

Despite physical contacts that might be present in some interactions, a key element in many biotic associations is the species's chemical arsenal. Many examples within the animal and plant kingdoms illustrate the importance of molecular dialogues between two or more interacting species, such as for plant-herbivore interactions (Erb and Reymond, 2019) or the mycorrhizal symbiosis (Hause and Fester, 2005). For Laboulbeniomycetes, the molecular mechanisms, as well as the chemical interactions with other species, remain a mystery. Very recently, Law (2024) presented the first annotation of a Laboulbniomycetes genome and predicted genes that are homologous with those of entomopathogenic species. One predicted gene matched to PR-1A proteins, which are known to be involved in pathogenicity, especially the formation of haustoria. This work sets the stage towards a new conceptual and methodological framework for the study of Laboulbeniomycetes interactions with other organisms, leveraging transcriptomic and proteomics tools.

For the case of Pyxidiophorales detected in environmental samples, metatranscriptomic, metaproteomic, and metabolomics approaches could be used to explore the interactions between Pyxidiophorales and the environment. Specifically, this includes the characterization of the molecular arsenal produced by Laboulbeniales and their hosts, which can help answer some fundamental questions, such as "*are there specific molecular dialogues and chemical recognition patterns between parasites and their hosts explaining the depicted high host specificity within Laboulbeniomycetes and the presence of penetration structures in specific taxa?* "

Given Laboulbeniomycetes is a class comprising study cases of obligatory associations, involving multiple interactions with other kingdoms and across trophic levels, gaining a deeper understanding of these biotic interactions could inform us about the functional roles of Laboulbeniomycetes within ecosystems and the evolutionary mechanisms that have shaped their diversity. Hence, the Eltonian shortfall might represent one of the most important knowledge lacunae to address for the Laboulbeniomycetes, but at the same time the most complicated to fill. To date, as for the Hutchinsonian shortfall, current knowledge about Laboulbeniomycetes interactions and the effects of parasitism on hosts are at the individual species level. This underscores the need for Laboulbeniomycetes to be observed through the prism of community and network ecology. However, as already noted for the other shortfalls, the study of Laboulbeniomycetes interactions with other species and biotic factors is impeded by the Linnean shortfall; the delimitation of species should be clearly established in order for reliable interpretations of host–parasite interactions to be made. Nevertheless, future research efforts to address the Eltonian shortfall have the potential to accumulate solid scientific-based evidence for protection measures that protect interaction networks in which Laboulbeniomycetes are involved.

# Parkerian shortfall

Despite its vital importance (Bartholomew, 1986), baseline natural history knowledge—which pertains to the descriptive study of singular and isolated biological cases (idiographic)—has been denigrated and is in decline, giving way to studies that seek to establish general, universal laws based on observed facts (nomothetic) (Cotterill and Foissner, 2010). One consequence of this shift is the lack of appreciation of fundamental taxonomic and descriptive works, suggesting that quantitative, hypothesis-driven, law and concept-based scientific works offer more valuable or fruitful contributions than descriptive ones. This tendency is sometimes even encouraged by scientific advisors to students (Bury, 2006). As a result, even for one of the most well-studied organismal groups, birds, lacunae in natural history knowledge persist for less studied species. Lees *et al.* (2020) underscored this specific gap for neotropical birds regarding foraging behavior and species diet; based on this, they designated this knowledge gap the Parkerian shortfall. Within the same year, Faria *et al.* (2020) introduced the Haeckelian shortfall, pointing out the knowledge gaps concerning "the distinct semaphoronts of a substantial fraction of all known species." Since this shortfall is about organismal ontogeny, we consider it to be part of the Parkerian shortfall, justifying our decision not to dedicate a full section to the Haeckelian shortfall in this chapter.

The lack of knowledge regarding species' natural history hinders efforts to (1) address other biodiversity knowledge shortfalls and (2) integrate poorly known organismal groups into IUCN Red List assessments (Bland *et al.*, 2017). This is because such knowledge informs species' morphological and phylogenetic delimitations, geographical distributions, and ecological interactions (Bogoni *et al.*, 2022). Laboulbeniomycetes, in particular, represent an organismal group where most of the body of knowledge is a matter of natural history. A key point is that alpha taxonomic knowledge is largely based on morphology, hence reliant on traditional observational descriptions that intrinsically contain general life history information on species. Foundational work in this area in relation to Laboulbeniomycetes are the unmatched contributions of Roland Thaxter (Thaxter, 1896, 1908, 1924, 1926, 1931), who described 1340 species (of which 1183 currently valid) (**Fig. 8**).

Figure 8: **One of the original, hand-drawn plates of Roland Thaxter—as a display of his craftsmanship—digitized by the Harvard University Botany Libraries.** Thaxter, R., 1896. Contribution towards a monograph of the Laboulbeniaceae [original plates]. Plate XIV (seq. 21). Oversize T3685cpo. Image courtesy of the Farlow Reference Library of Cryptogamic Botany, Harvard University. https://nrs.lib.harvard.edu/urn-3:fmus.far:101233803?n=21.

Life history knowledge has been instrumental to our current understanding of Laboulbeniomycetes evolution. This was especially the case for Pyxidiophorales, with *Pyxidiophora* potentially representing a missing link between Laboulbeniales and the other ascomycetes based on life history evidence (Blackwell and Malloch, 1989; Blackwell *et al.*, 2020). More generally, it was life history observations that initially placed Laboulbeniales within Ascomycota, which was later confirmed by other lines of evidence, including DNA (Haelewaters *et al.*, 2021a). On the other hand, phylogenetic relationships suggested by DNA cannot stand alone without being supported by other data, including taxonomic and life history information (Cazabonne *et al.*, 2022).

Several other studies have contributed to the accumulation of basic life history knowledge for Laboulbeniomycetes, including work on the influence of host activities and position specificity on thalli morphology, the culturability of Laboulbeniales, the effects of environmental conditions on Laboulbeniales growth (e.g., De Kesel 1996; De Kesel and Van Den Neucker 2005; Whisler 1968), and several other aspects of their life history. Faull (1905, 1906, 1911, 1912) was among the first to study and discuss the cytology of Laboulbeniales species. In particular, he devoted a 30-page paper to the cytology of *Laboulbenia chaetophora* and *L. gyrinidarum* (Faull, 1912). Although this piece was published more than a century ago, it remains one of the most detailed cytological investigations for a Laboulbeniomycetes species to date. Richards and Smith (1954, 1955a, 1955b, 1956) published a four-part comprehensive life history-oriented investigation for *Herpomyces*, which included a focus on histology, histopathology, host specificity, and morphological development. Hill (1977) was interested in the ultrastructure of*Herpomyces* sp. ascocarp, while Tavares (1965, 1966, 1970) was interested in the structure and development of *Amorphomyces* (Laboulbeniales) and *Herpomyces* spp. Later, Weir and Beakes (1996) focused on the morphological development of *He. virescens* sensu lato, using light and scanning electron microscopy.

It is noteworthy that works focusing on life history knowledge (e.g., cytology, development, histology, ontogeny, etc.) for Laboulbeniomycetes were mostly published during the late 19th and 20th centuries. Despite this publication peak, several natural history papers have been published in the 21st century. Recently, two papers presenting developmental studies of Indian Laboulbeniomycetes were published, illustrating and discussing different developmental stages of *Dimeromyces anisolabis*, *Peyritschiella furcifera*, and *P. vulgata* (Narang *et al.*, 2023; Shukla and Narang, 2024). We can also mention the histopathology studies discussed for the aforementioned Eltonian shortfall. Even if natural history knowledge is the foundation of laboulbeniology, this knowledge is available for only a limited number of Laboulbeniomycetes taxa. Very few studies overall have contributed to accumulating natural history knowledge for Laboulbeniomycetes.

Laboulbeniology may indeed benefit from more monothetic studies, yet it clearly demonstrates the importance of idiographic knowledge in enhancing our understanding of poorly known organismal groups. Addressing the Parkerian shortfall necessitates the recognition of the priceless value of basic natural history information (Lees *et al.*, 2020). This aligns with the need for greater appreciation of such fundamental work within both the scientific community and society at large. We therefore encourage researchers to value all forms of natural history work, particularly for understudied organisms, such as taxonomic notes and species checklists. Using Laboulbeniomycetes as an example, we further call for increased research efforts directed towards the natural and life history aspects of organisms. This includes, for example, allocating more resources for conducting biodiversity inventories, and taxonomic, observational and descriptive projects. Specifically, we champion the leveraging of the promising potential offered by citizen scientists and museum collections to fill this particular shortfall.

## Latimerian shortfall

Quantifying extinction risk is an important IUCN criterion for assessing the threatened status of a given species. However, the question of "*when we can consider a taxon extinct* " remains a debated subject. According to the IUCN (2012), a taxon is classified as extinct when "there is no reasonable doubt that the last individual of a species has died." However, this can rarely be determined with full certainty and is prone to subjectivity (Roberts *et al.*, 2023). In this regard, one piece of information that can inform extinction risk is the 'last seen' or 'last sighting' date. This information indicates when a species was last reliably observed, and a species can be considered lost if it has not been sighted in the last 50 years, although some use a threshold of 10 years (Long and Rodríguez, 2022; Martin *et al.*, 2023a). Despite the value of keeping track of lost species, it nevertheless remains uncertain whether species that have not been observed for many years or decades are truly extinct or still extant.

‘Lost’ taxa raise important conservation issues for both well-studied and understudied organismal groups in the context of the Anthropocene extinction crisis. Martin *et al.* (2023a) recently proposed a new knowledge shortfall related to lost species: the Latimerian shortfall. They conducted the first quantitative assessment of the number of lost species of terrestrial vertebrates, finding 1.7% of all species assessed could be considered lost. Subsequently, Haelewaters *et al.* (2024) performed the second published quantitative assessment of the Latimerian shortfall for an organismal group (and the first focused on an understudied taxa), the Laboulbeniomycetes. One observation that resulted from these two studies is that the proportion of lost species depends on the organismal group and whether they are considered well or poorly studied. The number of lost species for Laboulbenioimycetes, in the sense that there has been no reliable observation over 50 years, was clearly higher than the number of lost species within vertebrate groups (51% versus 1.7%), with most lost Laboulbeniomycetes species last seen between 80 and 130 years ago, peaking at 100–109 years ago (**Fig. 9**). This peak in the number of lost Laboulbeniomycetes has been attributed to the work of Roland Thaxter (i.e., the ‘skewed specialist effect’). For instance, the majority of currently valid species in the class were described by Roland Thaxter between 1891 and 1931. Many of these have not been reported since, with nearly three-quarters of all Laboulbeniomycetes species lacking reliable observation after initial description (Haelewaters *et al.*, 2024). This underscores the point that for understudied organismal groups such as the Laboulbeniomycetes, the ‘last seen’ information may reflect a lack of expertise more than evidence of biological extinction. A given taxon might not have been observed for decades because too few people are working on this specific group, and only a handful of people are suitably qualified to be able to report new observations. For example, *Laboulbenia temperei* has not been observed since its initial description from France by Balazuc (1973), until its rediscovery 49 years later by De Kesel *et al.* (2022) in Belgium. If this species had not been reported by De Kesel *et al.*, in 2024 it would have been considered a lost species, considering a threshold of 50 years.

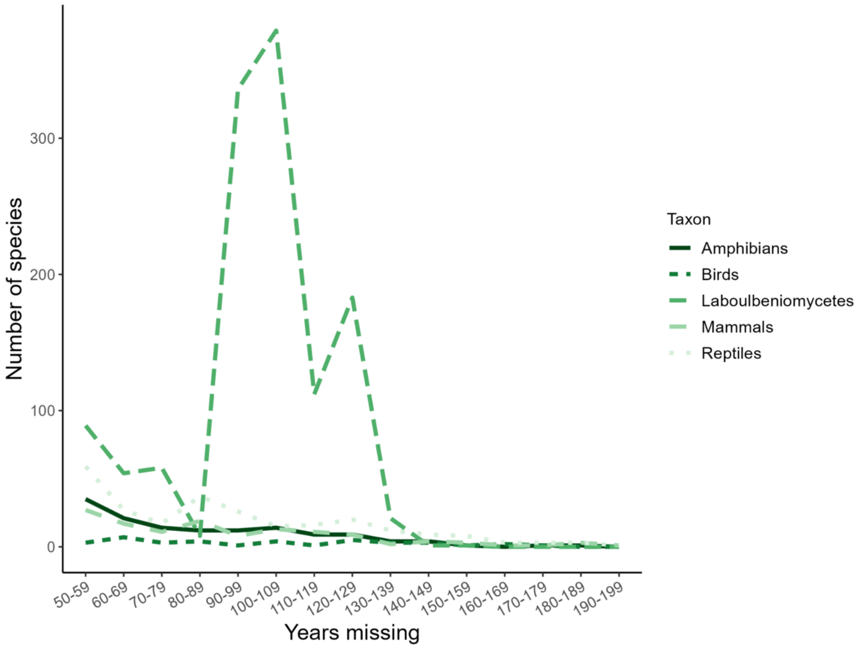

Figure 9: **Last seen dates for lost amphibian, bird, Laboulbeniomycetes, mammal, and reptile species, from Haelewaters *et al.* (2024).**

We assume that the above-mentioned example is not an isolated case; many Laboulbeniomycetes species currently considered lost are likely to be eventually rediscovered. If this proves to be a generalizable pattern, it raises serious conservation issues for Laboulbeniomycetes and other understudied groups, given it can be hard to effectively conserve an organismal group when it is unknown whether most of its species are extant or truly extinct. If such species remain lost, no information about their ecology, interactions, and geographical distribution will be known, hence impeding the filling of other related knowledge shortfalls and the integration of poorly known species into conservation strategies.

To advance towards an effective framework for lost species (Martin*et al* . 2023b), particularly one that is relevant to understudied organismal groups, we encourage discussions about the terminology of how a lost species should be defined, as well as when a species should be considered 'last seen', considering that some organismal groups can be more subject to a 'skewed specialist effect' than others. Moreover, we advocate for discussions about what can be considered a rediscovery of a lost species, such as direct field observations, citizen-science platforms, or eDNA (Martin *et al.*, 2023b). Indeed, to state that a Laboulbeniomycetes species has been rediscovered, *should the report be supported by morphology, genetics, or both?* Furthermore, *it is possible that several Laboulbeniomycetes species could be rediscovered thanks to eDNA, but is this sufficient evidence?*

These questions highlight the need to clarify the taxonomy of Laboulbeniomycetes, as numerous lost species in this class are known only from their types (i.e., case of singletons, see Cazabonne *et al.*, 2024) and may pose challenging systematic placement. It is possible that some of these lost species are actually placed in currently recognized species complexes, but due to diverging morphotypes, such species will be formally rediscovered only when molecular data eventually reveal that they represent the same species. Moreover, some lost Laboulbeniomycetes species may actually be present in already established museum/institutional collections or in photographs posted on social media or citizen science online platforms. Museum entomological collections and citizen science efforts have already led to the description of new Laboulbeniales species; consequently, the rediscovery of lost species might also be possible. Encouraging the resolution of species complexes and leveraging still largely untapped diversity pools within museum collections and citizen science initiatives could help to reduce the Latimerian shortfall for Laboulbeniomycetes and, by the same rationale, the other related shortfalls.

It has been predicted that the Latimerian shortfall will become increasingly important as the Anthropocene progresses (Martin *et al.*, 2023a). The issue of lost species and their conservation has been previously discussed for animals and the specific fungal groups of the Laboulbeniomycetes. However, many other well-studied and poorly known organismal groups could also benefit from such discussions. We urge the scientific community to quantitatively assess the lost species shortfall for other organismal groups. A comparison of the prevalence of lost species and their potential for rediscovery among understudied and well-studied groups may help us determine whether the patterns of lost species observed in Laboulbeniomycetes are characteristic of understudied groups in general, and the extent of a potential skewed specialist effect in other groups. If such efforts are not undertaken rapidly at a global scale and across kingdoms, many species that are currently considered lost but are actually still extant may become truly extinct due to global change.

## Scottian shortfall

The categorization of threats by the IUCN serves as a crucial instrument for devising species conservation strategies and action plans. The IUCN Red List criteria have been widely applied to animals and plants, encompassing regional and global red list assessments for several well-studied organismal groups therein. For example, birds, conifers and cycads are examples of organismal groups where all species have been evaluated based on IUCN criteria. Comprehensive global assessments have also been initiated for mammals and amphibians (Rodrigues *et al.*, 2006). Notably, amphibians have undergone global assessments by the IUCN twice (Re:wild, Synchronicity Earth, IUCN SSC Amphibian Specialist Group, 2023). The IUCN has also commenced assessments of extinction risks for the world's reptiles (Meiri *et al.*, 2023) and marine (Polidoro *et al.*, 2009) and freshwater fish species (Carrizo *et al.*, 2013).

Despite the IUCN Red Listing being regarded as a benchmark for prioritizing species-level conservation, many understudied organismal groups have remained unassessed for several years since its inception. This is particularly true for the fungal kingdom. It took nearly 40 years for the first fungal species (i.e., lichens) to be incorporated into the IUCN Red List (Mueller *et al.*, 2022). While several other fungal species have now also been assessed, fungi remain one of the most neglected organismal groups within IUCN Red List assessments. As of June 27, 2024, 794 fungal species have been assessed, with Agaricomycetes and Lecanoromycetes being the best represented fungal groups (IUCN, 2024). This represents a 33% increase (i.e., 197 added) compared to the 597 fungal species published in 2022 (Mueller *et al.*, 2022). However, much work remains to be done, considering the estimated total number of fungal species and the current bias to fungi forming large, macroscopic spore-bearing structures (Gonçalves *et al.*, 2021).

As part of a growing momentum for the integration of fungi into conservation frameworks, several initiatives have been proposed to conduct global assessments of fungal species. One such initiative is the Global Fungal Red List Initiative (GFRLI), established in 2013. The GFRLI is a pivotal platform for mycologists to discuss, share, and propose new fungal names for inclusion in the updates of the IUCN Red List. Several actions and workshops have been conducted under the GFRLI, focusing on specific fungal groups and geographical regions. These include Basidiomycota, Agaricomycetes, lichens, rusts and smuts, edible mushrooms, Mediterranean fungi, Chanterelles, and EDGE species. The GFRLI also includes several specialist groups that cover macrofungal groups such as mushrooms, brackets and puffballs, lichens, cup-fungi, truffles and allies, as well as microfungi groups including chytrids, zygomycetes, downy mildew and slime molds, rusts and smuts. Pioneering specialist groups within the IUCN Species Survival Commission (SSC) have been established specifically to contribute to the conservation of Brazilian and Columbian fungi. Recently, a new specialist group was created through the funded Biodiversa+ project FUNACTION, focusing exclusively on a unique ecological group of fungi: aquatic fungi (Fernandes *et al.*, 2024). These initiatives are highly promising and should be pursued, particularly given that the IUCN has acknowledged taxonomic gaps in their Red Listing of fungal species. According to the IUCN Red List 2021–2030 Strategic Plan, a total of 23,500 additional assessments of fungal species is projected by 2030 (IUCN 2021).

The shortfall related to the number of species assigned a threat category on the IUCN Red List within an organismal group was recently identified and described as the Scottian shortfall (Haelewaters *et al.*, 2024), named after Sir Peter Markham Scott (1909–1989) in honor of his involvement in the establishment of the Red List. It is closely related to the Ostromian shortfall (discussed below): the gaps in conservation assessments, methods, funding, and policies (Lopes-Lima *et al.*, 2021). Notably, this is the first described knowledge shortfall (sensu Hortal *et al.*, 2015) based on a fungal group, as the Latimerian and Ostromian shortfalls were described based on terrestrial vertebrates and freshwater molluscs, respectively. Unlike the Ostromian shortfall, the Scottian shortfall is highly quantitative, being expressed as the difference between the number of described species in a group and the number of species that have received an assessment by the IUCN Red List. The Laboulbeniomycetes are an example of a complete (100%) Scottian shortfall: not a single member of the class is IUCN Red Listed (**Fig. 10**).

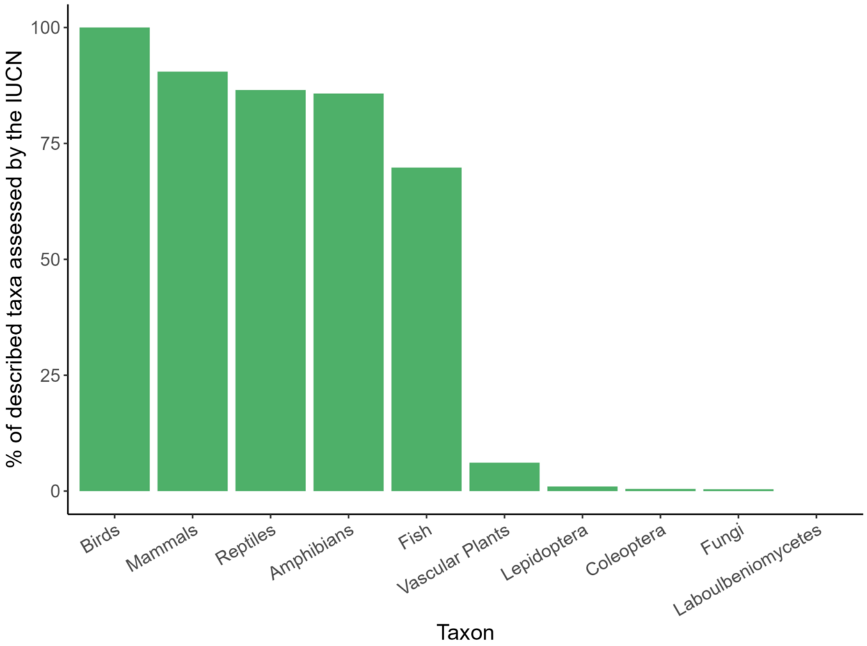

Figure 10: **Proportions of described species in selected taxa that have been assessed by the IUCN, from Haelewaters *et al.* (2024).**

Even if assessed, many of the Laboulbeniomycetes species would likely be classified as data deficient. This can be explained by the multiple substantial aforementioned knowledge shortfalls related to geographical distributions and population sizes. This lack of IUCN assessments could impede the integration of Laboulbeniomycetes into conservation plans (Haelewaters *et al.*, 2024). Assigning data deficient categories to Laboulbeniomycetes species could, however, still be a valuable initial step to point out areas where research, knowledge gap filling, and conservation efforts should be directed. Moreover, some Laboulbeniales species that have less marked shortfalls (comparatively to the other Laboulbeniomycetes species) can be promising candidates for targeted research efforts and an IUCN assessment, such as *He. harmoniae*. Furthermore, as a model study system for host-parasite interactions, efforts to fill the Scottian shortfall for the Laboulbeniomycetes could pave the way for the broader integration of fungal parasites in IUCN assessments, or the inclusion of a specialist group within the IUCN SSC.

# Ostromian shortfall

The representation of lesser-known organismal groups in conservation strategies, such as protected areas, depends on factors beyond IUCN species assessments. These factors include the conservation statuses of habitats and ecosystems, decision-making and legal policies, availability and accessibility of funds, and the awareness of the general public and policymakers. The gaps related to all these factors have been collectively termed the Ostromian shortfall (Lopes-Lima *et al.*, 2021).

**Protection of interaction networks**. The conservation of understudied organismal groups such as Laboulbeniomycetes could be enhanced by integrating them into community, habitat, and ecosystem conservation statuses. However, this approach is hindered by the many knowledge gaps for Laboulbeniomycetes and the complexity of attributing threat statuses to communities, habitats, and ecosystems, given the wide diversity of interaction networks (Tylianakis *et al.*, 2010; Keith *et al.*, 2013). The IUCN has launched a program to assess the threat status of ecosystems, the Red List of Ecosystems (RLE) (`https://iucnrle.org`), which includes five criteria: reduction in geographic distribution, restricted geographic distribution, environmental degradation, disruption of biotic processes or interactions, and quantitative analysis that estimates the probability of ecosystem collapse (Keith *et al.*, 2013).

The presence of Laboulbeniomycetes in a given ecosystem is heavily influenced by the presence of their habitats. For instance, Laboulbeniales ectoparasites are presumed to be found in the same ecosystem as their hosts, especially if the association is highly specific. Therefore, we can assume that protected areas that incorporate insect and arthropod habitats would also provide protection for their associated Laboulbeniomycetes. However, a decline in the number of individuals in natural populations of insects has been observed, and some studies report that insect species are inadequately represented in protected areas (Chowdhury *et al.*, 2023). This can impact the representativeness of Laboulbeniomycetes in ecosystem and habitat conservation programs. Narrow habitat specialists and species with restricted ranges, such as many arthropod species and Laboulbeniomycetes species, are underrepresented in habitat conservation prioritization (see Cardoso *et al.*, 2011).

The response of Laboulbeniomycetes to global environmental change, including climate change and habitat loss, remains unknown. This information is essential, alongside baseline data on species assemblages and communities in untouched ecosystems, for the integration of organisms in management and conservation plans. For Laboulbeniales ectoparasites, it can be hypothesized that the influence of human-induced environmental changes on their hosts may have yet-to-be-determined effects on the parasites. The two main insect families that host Laboulbeniales parasites, Carabidae and Staphylinidae, are known to be affected by habitat fragmentation. These insect groups have important implications for biodiversity conservation in mature and late successional forests (Niemelä, 2001; Pohl *et al.*, 2007). Further studies are needed to investigate the differences in Laboulbeniomycetes species presence, community assemblages and ecological roles between untouched, reference ecosystems and ecosystems impacted by anthropogenic disturbances.

Considering Laboulbeniomycetes in community, habitat, and ecosystem conservation frameworks brings forth the concept of cascade effects (Sanders *et al.*, 2018). This concept is understood in the sense that if species A interacts directly and obligatorily with species B, protecting species A means protecting species B. Conversely, if species A is vulnerable to global change or goes extinct, so does species B. This highlights the need to consider Laboulbeniomycetes in the context of protecting interaction networks, not just individual species. This implies that knowledge gaps for the Laboulbeniomycetes will only be fully addressed when those for their hosts and habitats are also tackled. An initial step we propose is to evaluate the IUCN Red List statutes of known arthropod hosts of the Laboulbeniales to infer their potential threat and conservation statuses. Substantial efforts should be directed towards this goal, as in 2006, less than 0.1% of described insects had received an IUCN Red List assessment (Rodrigues *et al.*, 2006), and while this figure had risen to 1.2% by 2024 (IUCN 2024), an enormous about of work remains to be completed in this area.

There is a discrepancy in IUCN assessments among the main Laboulbeniales host orders, which might guide preliminary efforts. For example, Coleoptera, the insect order from which most Laboulbeniales are known, is the insect order with the second-most assessed species (1882). This is of course somewhat relative because the diversity of beetles is very high with 327,597 described species (meaning that 0.57% are IUCN Red List-assessed). Likewise, for Blattodea, hosts of Herpomycetales, 0.53% of described species are IUCN Red List-assessed, while for Diptera, the insect order from which 10% of Laboulbeniales are known, only 0.21% are. This is to illustrate that many host taxa of Laboulbeniomycetes also have a significant Scottian shortfall, lacking IUCN assessments or being data deficient. For instance, the main known hosts of *R. wasmannii*, such as *M. sabuleti* and *M. scabrinoides*, as well as the host of the widespread *He. harmoniae*, *Ha. axyridis*, have not yet been assessed by the IUCN. The recently described *Rhachomyces spiralis* (Rossi and Leonardi, 2020) was found on *Guizhaphaenops* sp. (Coleoptera, Carabidae) in China; all species of this genus that have been assessed thus far (10 species) are data deficient.

This same line of reasoning can also be applied to tripartite interactions involving Laboulbeniales. For example, considering only the systematic survey of the distribution of bat fly-associated Laboulbeniales in Central Europe by Haelewaters *et al.* (2017a), all bats found to be carrying infected bat flies were IUCN assessed and were classified as either vulnerable (*Miniopterus schreibersii*), near threatened (*Rhinolophus euryale*), or least concern (*Myotis daubentonii* and *Myotis myotis*). Nevertheless, we believe that these aspects of interaction networks, cascade effects, and co-extinctions will be some of the most important entry points for Laboulbeniomycetes into conservation frameworks.

**Legal policy**. Although fungi have been largely neglected within conservation frameworks, there has been a growing momentum to integrate fungi into legal policies and decision-making processes. In the mid-1980s, pioneering efforts to change the perception of fungi in conservation were initiated through the European Council for the Conservation of Fungi (ECCF,`http://www.eccf.eu/welcome-en.ehtml`). This was followed by the inclusion of fungi in regional, national, and global IUCN assessments, the establishment of IUCN fungi-focused specialist groups, and the GFRLI (Mueller and Allen, 2023). A subsequent milestone was the triple F initiative. Paralleling Fauna and Flora, Kuhar *et al.* (2018) introduced the term Funga to designate the fungi of a specific region, habitat, or geological period, thereby facilitating the integration of mycology into conservation and education goals. Fungi are increasingly recognized as vital components of ecosystem functionality and health. This is exemplified by Re:wild and the SSC, which were the first global organizations to officially adopt a mycologically inclusive language in their public communications, followed in 2024 by the National Geographic Society, that revised their definition of wildlife to include fungi (`https://www.nationalgeographic.org/society/our-focus/wildlife/`). This global recognition of fungi was further confirmed at the European level in 2023, with the European Union revising their definition of ecosystem as "a dynamic complex of plant, animal, and fungi and microorganism communities and their non-living environment, interacting as a functional unit, and includes habitat types, habitats of species and species populations" (`https://data.consilium.europa.eu/doc/document/ST-10445-2023-INIT/en/pdf`). In addition to these advances, several open letters have been published to increase global appreciation of fungi among policymakers (Gonçalves *et al.*, 2021; Palahí *et al.*, 2022).

Despite these milestones, there remains a significant Ostromian shortfall for fungi in terms of representativeness within legal policies. Through the term Funga and the inclusion of fungi in environmental definitions, Laboulbeniomycetes and other understudied fungal groups are *de facto*indirectly included. However, to date, there are no legal policies or environmental laws that officially state and recognize the need to specifically integrate understudied fungal groups into conservation frameworks. A legal framework for the protection of Laboulbeniomycetes is, therefore, non-existent. Given the accumulated knowledge regarding the taxonomic and ecological diversity of understudied fungal groups, we believe conservation perspectives recognizing fungi as an independent kingdom and expressing a willingness to protect it should be considered in light of current knowledge shortfalls. A way forward for understudied fungal groups in global conservation frameworks and legal policies might be enhanced by (1) considering fungi on an equal footing with animals and plants, (2) recognizing the prevalence of understudied groups that are phylogenetically and ecologically unique within the fungal kingdom, and (3) focusing efforts to fill the Ostromian shortfall.

**Funding**. A limiting factor in addressing all aspects of the Ostromian shortfall for Laboulbeniomycetes is the availability and accessibility of funding. Uncharismatic species, and those that do not present evident economic or emotional interests to humans, are unlikely to be the focus of conservation programs or to receive funding in comparison to more charismatic species (Colléony *et al.*, 2017; Lopes-Lima *et al.*, 2021). For the EU LIFE-Nature program, poorly known and speciose organismal groups, such as arthropods, receive significantly less funding compared to better-known groups like mammals and birds (Cardoso *et al.*, 2011). The Mohamed bin Zayed Species Conservation Fund allocates grants for individual species conservation initiatives; of the 1,828 species supported thus far, only 59 are fungi (= 3.2%). Unsurprisingly, no Laboulbeniomycetes are included among these.

Securing funding for research projects focused on Laboulbeniomycetes and other understudied groups is extremely challenging. Such funding is more likely to be obtained by proposals and rationale that are monothetic and related to broad ecological and evolutionary conceptual frameworks. Indeed, it is difficult to obtain financial support for organismal groups with severe knowledge shortfalls, especially in terms of species descriptions, geographical distributions, lost species, and conservation status assessments, as this means proving they represent a conservation priority is difficult (Haelewaters *et al.*, 2024). It is particularly crucial to call for increased financial allocations to explorative biodiversity studies aiming to fill knowledge shortfalls for species-rich and understudied organismal groups. This is because it is within these groups that a lack of knowledge will most hinder conservation assessment efforts (Hochkirch *et al.*, 2021). Awareness should be raised about these disparities among organismal groups to ensure that overlooked organisms are not further underestimated in conservation programs and by conservationists (Titley *et al.*, 2017).

**Awareness and communication**. Another aspect of the Ostromian shortfall for the Laboulbeniomycetes is the lack of awareness among the general public and policymakers, as well as the lack of communication about these understudied organisms. Public awareness and societal preferences can influence research efforts (Guedes *et al.*, 2023), and taxa that garner more public interest generally receive more funding (Troudet *et al.*, 2017). Most people are not aware of the wide taxonomic, ecological and interaction diversity of Laboulbeniomycetes; even among the scientific community, only a small number of mycologists, entomologists, and parasitologists have observed specimens under a microscope and are aware of their existence. This lack of awareness can be partly attributed to the insufficient scientific communication and popularization of understudied organisms. Laboulbeniomycetes are suitable candidates for educational campaigns and could pave the way for other understudied organismal groups to gain the interest of the public, policymakers, and scientists.

Laboulbeniomycetes exhibit a large diversity of forms that can convey appealing images to the general public, thereby sparking interest in overlooked organisms. Due to their lifestyle on host cuticle, Laboulbeniales microfungi were colloquially referred to as “beetle hangers” by Mordecai C. Cooke in the nineteenth century (Cooke, 1892; Haelewaters *et al.*, 2021a; de Groot *et al.*, 2024). Today, Laboulbeniomycetes are also colloquially known as “labouls”. These colloquial terms can facilitate efficient and accessible communication with the general public and policymakers. The terms “beetle hangers” and “labouls” have been used to name the website dedicated to Laboulbeniales research, beetlehangers.org, and the research team working on Laboulbeniomycetes, TeamLaboul, respectively. The distinctive, bizarre, and otherworldly (Haelewaters *et al.*, 2021a) morphologies of Laboulbeniomycetes can be an entry point for people to learn about this class. For instance, *Zodiomyces rhizophorus* (**Fig. 11**), described from Thaxter’s slide collections, is considered one of the largest and weirdest Laboulbeniales species (Rossi *et al.*, 2016; Haelewaters *et al.*, 2021a). This species presents a crown of appendages that resemble firework trailing. Although the species name does not refer to this spectacular feature, it inspired the title of the paper formally describing it, “*Fireworks under the microscope* ” (Rossi *et al.*, 2016). To take another example, Van Caenegem *et al.* (2023a) described and named a species of *Gloeandromyces*, *G. plesiosaurus* (**Fig. 11**), after its otherworldly appearance; the thallus resembles *Plesiosaurus*, a genus of extinct aquatic reptiles.

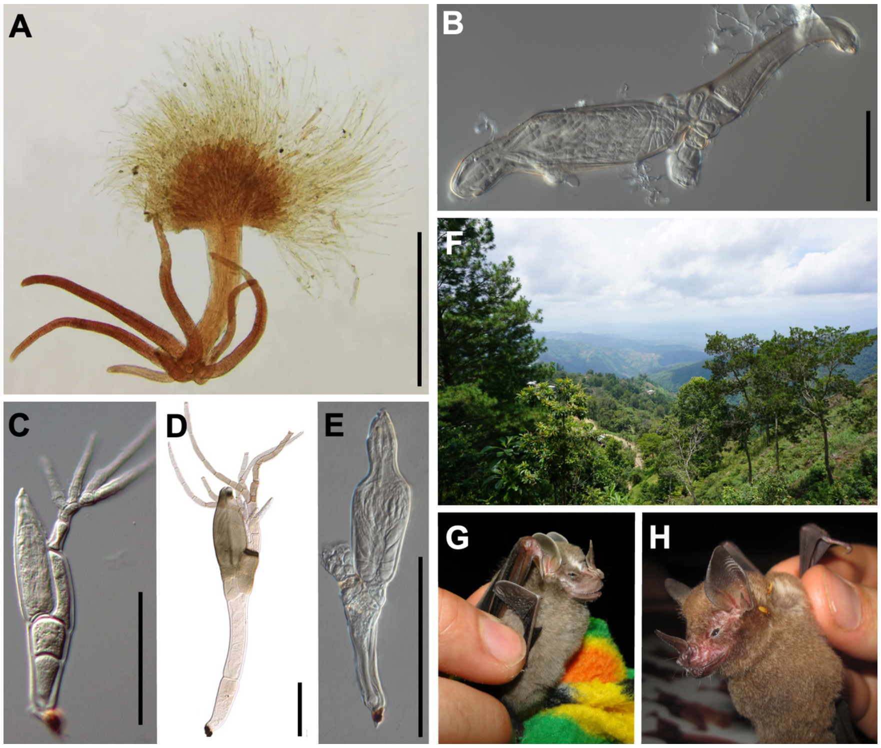

Figure 11: **A**. *Zodiomyces rhizophorus*. **B**. *Gloeandromyces plesiosaurus*. **C**. *Troglomyces twitteri*. **D**. *Laboulbenia quarantenae*. **E**. *Gloeandromyces cusucoensis*. **F**. Parque Nacional Cusuco (Honduras). **G**. Pygmy fruit-eating bat *(Artibeus phaeotis)*. **H**. *Carollia perspicillata* with two bat flies (Panama). Scale bars: **A** 500 µm, **B**–**C** 50 µm, **D**–**E** 100 µm. Photos: **A** Rossi *et al.* (2016); **B**, **F**–**H** Danny Haelewaters; **E** Van Caenegem *et al.* (2023a); **C** Santamaria *et al.* (2020); **D** Haelewaters and De Kesel (2020).

Laboulbeniomycetes species named after internationally-known societal events, periods, or platforms may garner more interest from the general public than species named after morphological features that would only be meaningful to experts. For example, *L. quarantenae*(**Fig. 11**) was named after the quarantine period initiated to curb the spread of the coronavirus 2 (SARS-CoV-2) at the origin of the COVID-19 global pandemic (Haelewaters and De Kesel, 2020). *Troglomyces twitteri* (**Fig. 11**) was named after the social media platform Twitter (now X), where this species was first observed (Santamaria *et al.*, 2020). These two Laboulbeniales species have been the subject of numerous newspaper articles worldwide. Moreover, Laboulbeniomycetes can be found in “outstanding” ecosystems or habitats that have high conservation and cultural value, including remote cloud forests (Haelewaters *et al.*, 2021d; Van Caenegem *et al.*, 2023a) and drumlin archipelagos (Haelewaters *et al.*, 2015c, 2019a) (**Fig. 11**). Furthermore, species that interact with Laboulbeniomycetes and that can be considered more “charismatic” can constitute an interesting gateway to introduce Laboulbeniomycetes to the general public and policymakers, such as Laboulbeniales associated with ladybirds (*He. virescens* species complex) and tropical American bats (**Fig. 11**). Lastly, Laboulbeniomycetes can reach a larger audience through various tools that are being leveraged to study them, such as natural history museum collections, citizen science, eDNA, and artificial intelligence (AI), as well as their benefits to human societies, such as via the biological control applications for invasive insect populations currently under exploration for *He. harmoniae* and *Ha. axyridis* (Haelewaters *et al.*, 2021a).

A first step towards filling these aspects of the Ostromian shortfall is to evaluate the awareness of Laboulbeniomycetes among the general public, policymakers, and scientists. This can be achieved through surveys targeting a broad audience. Afterwards, various means can be leveraged to communicate and raise awareness about Laboulbeniomycetes, including written, oral and visual communication. Besides peer-reviewed scientific articles, writing popular science pieces could help disseminate general knowledge and scientific issues about Laboulbeniomycetes to a larger, non-expert audience in different languages. For instance, a popular science article in Czech by Koukol and Haelewaters (2021) (`https://ziva.avcr.cz/2021-1/laboulbeniales-nejprapodivnejsi-houbovi-paraziti.html`) has contributed to this effort.

Visual communication, such as drawings and illustrations, is another means of raising public awareness of Laboulbeniomycetes as people are more likely to take an interest in organisms that evoke emotions (Stankey and Schindler, 2006; Shine, 2011). Existing visual illustrations for Laboubeniomycetes, such as the #TeamLaboul logo (`https://beetlehangers.org`) and the illustration of *He. harmoniae* by Linshan Feng (Leiden University) in de Groot *et al.* (2024), could be utilized to address parts of the Ostromian shortfall. Moreover, high-quality images of Laboulbeniomycetes can be used to raise awareness within the scientific community. This can be achieved through various means, such as front cover pictures in large-audience, broad thematic journals. For instance, Laboulbeniomycetes featured on the front cover of an issue of the *Journal of Biogeography* for the first time in January 2024 (Haelewaters *et al.*, 2024, vol 51 issue 1 (`https://onlinelibrary.wiley.com/doi/10.1111/jbi.14635`). However, since most Laboulbeniomycetes species lack high-quality, publicly available visual illustrations—a shortfall recently described as the Keartonian shortfall and illustrated with bees (Marshall *et al.*, 2024)—effective visual communication to help fill the Ostromian shortfall may be lacking. Increasing efforts to document the diversity of Laboulbeniomycetes and other understudied organisms will necessitate the accumulation of high-quality illustrations to support communication and conservation actions.

Beetlehangers.org is intended to serve as a cornerstone of Laboulbeniales research for both scientists and the general public (de Groot *et al.*, 2024). Although currently focused on *He. harmoniae* on *Ha. axyridis*, this website is poised to become a powerful tool for raising public awareness about understudied organismal groups and increasing public knowledge about parasitic fungal diversity. It may also serve as a central platform for sharing written and visual communications about Laboulbeniomycetes in general, thereby getting people to know about the extent of our knowledge shortfalls on biodiversity and conservation.

## Introducing a new knowledge gap in light of understudied organismal groups: the Thaxterian shortfall

Laboulbeniomycetes represent a case study example of an understudied organismal group characterized by multiple knowledge shortfalls. Indeed, as demonstrated, all formally described knowledge shortfalls to date are applicable to Laboulbeniomycetes. Such groups have a heavy Linnean shortfall which inevitably leads to profound consequences on interrelated intrinsic (Eltonian, Hutchinsonian, Raunkiaeran) and extrinsic knowledge shortfalls (Wallacean, Prestonian, Darwinian). However, our exploration of shortfalls for Laboulbeniomycetes for this chapter led us to realize that further shortfalls need to be described with respect to poorly known organisms.

Most previously described shortfalls relate to the nature of the missing data/information itself, such as taxonomic diversity (Linnean), geographical distribution (Wallacean), population dynamics (Prestonian), evolution (Darwinian), functional roles (Raunkiaerian), abiotic tolerances (Hutchinsonian), ecological interactions (Eltonian) and natural history (Parkerian). On the other hand, the Latimerian and Scottian shortfalls can, to some extent, be considered a consequence of such data shortfalls; e.g., the heavy knowledge shortfalls of the Laboulbeniomycetes result in insufficient data to determine if a given species is truly lost and to provide most species with IUCN Red List assessments. The Ostromian shortfall encompasses both causes (lack of fundings, methods, awareness) and consequences (lack of conservation actions and legal policies) of these data shortfalls. Nevertheless, Laboulbeniomycetes highlight an as yet undescribed shortfall that is interconnected to all the other shortfalls and can be considered one of their main causes: the lack of taxonomic expertise (**Fig. 12**). This gap was already identified by Haelewaters *et al.* (2024) as the 'skewed specialist effect', although not formally named.

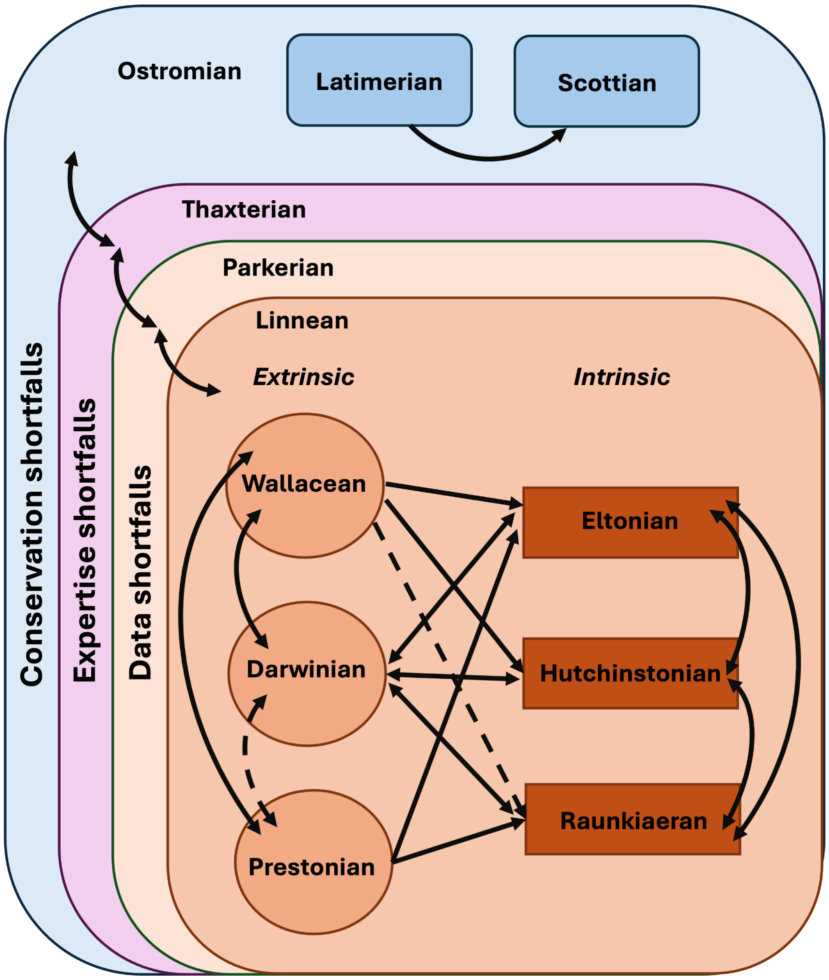

Figure 12: **Relationships between knowledge shortfalls.** Relationships among the Linnean, Wallacean, Darwinian, Prestonian, Eltonian, Hutchinstonian, and Raunkerian shortfalls are modified from Hortal *et al.* (2015). Different shades of orange reflect different levels of complexity among data shortfalls, with the basic, fundamental Linnean shortfall and the more complex extrinsic and intrinsic shortfalls. Similarly, as the extrinsic and intrinsic shortfalls are heavily dependent on the Linnean shortfall, the latter is in turn dependent on basic natural history knowledge (Parkerian shortfall). All these data shortfalls are successively dependent on expertise shortfalls (newly introduced Thaxterian shortfall for taxonomic expertise); without experts to collect basic data, the latter inevitably have subsequent shortfalls. Both expertise and data shortfalls are interrelated with conservation shortfalls.

We propose to formally describe this gap in taxonomic expertise: the Thaxterian shortfall, named after Roland Thaxter (1858–1932) who described 48% of all currently valid Laboulbeniomycetes species (Haelewaters *et al.*, 2024) (**Fig. 13**) and facilitated a strong 'skewed specialist effect' after his death (**Fig. 9**). Thus, his academic career is representative of the factors that create this shortfall. The fact that Roland Thaxter's work was instrumental in our understanding of Laboulbeniomycetes diversity is particularly well illustrated within the Herpomycetales: he described 85% (23 species out of 27) of known species of *Her-*

*pomyces*. This shortfall can be interpreted as the proportion of species in a given organismal group that have been described by a single or a handful of descriptors. It can be quantitatively expressed as the number of species descriptions per taxonomist in a given organismal group. The Thaxterian shortfall is the second knowledge gap formally described based on a fungal study case. We encourage the scientific community working on biodiversity and conservation shortfalls to address this Thaxterian shortfall for other organismal groups, notably to provide sufficient quantitative assessments to compare this specific taxonomic shortfall between well-studied and less-studied organismal groups. We also encourage further studies to plot the number of described species per taxonomists over time to explore if the 'skewed specialist effect' is a generalizable pattern among poorly known organismal groups.

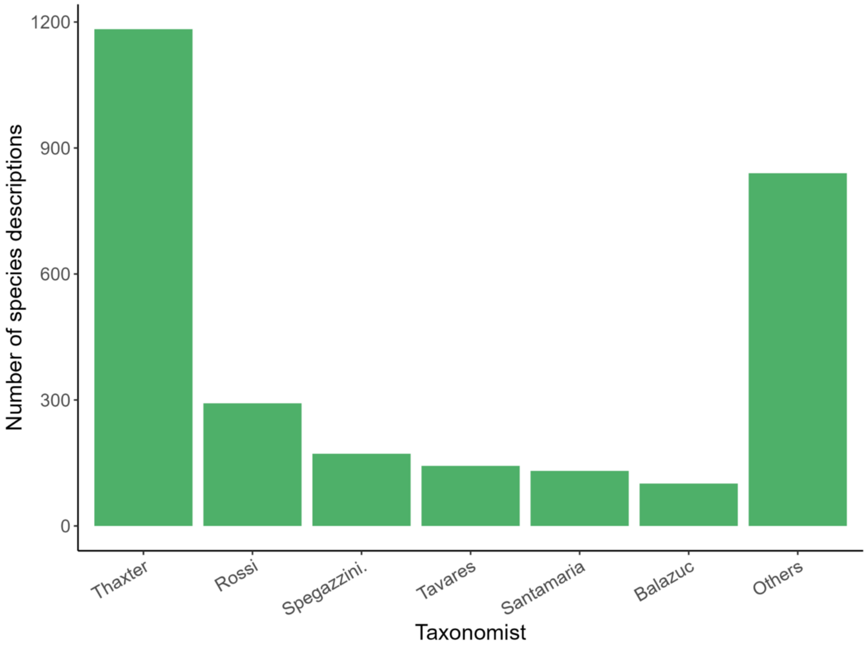

Figure 13: **Number of species descriptions per taxonomists for the Laboulbeniomycetes, edited from Haelewaters *et al.* (2024).**

# Summary points

1. Laboulbeniomycetes represent a textbook example of poorly known organisms with multiple interconnected knowledge, biodiversity and conservation shortfalls.
2. Addressing the Linnean shortfall is the highest priority, given that resolving the other shortfalls largely hinges on discovering and describing all taxa. New species of Laboulbeniomycetes will be discovered through fieldwork in undersampled geographic areas and habitats as well as through screening of dried pinned arthropod collections.
3. Multi-locus phylogenetic and genome-scale analyses will improve our current understanding of the Laboulbeniomycetes tree of life, resolve their evolutionary relationships among other Ascomycota taxa, and unravel the molecular basis of morpho-developmental patterns.
4. An eDNA-based framework is needed to understand the gaps in Laboulbeniomycetes diversity, geographical distribution, evolution, ecological interactions, and responses to environmental changes.
5. Increasing collaborations between researchers and citizen scientists will be instrumental in addressing sampling biases and raising public awareness about Laboulbeniomycetes.

6. Recognizing, funding, and promoting fieldwork and the accumulation of basic taxonomic and natural history knowledge is essential to support efforts towards reducing biodiversity and conservation shortfalls.

# Future research

This chapter underscores the need to address knowledge shortfalls for understudied organismal groups, especially in the face of current global environmental changes. In this context, challenges associated with filling the above-mentioned shortfalls must be overcome. These shortfalls reflect a concerning reality: fieldwork is declining in perceived importance and taxonomy has become a threatened discipline (Paknia *et al.*, 2015; Ríos-Saldaña *et al.*, 2018; Sago and Gaston, 2025). Therefore, we call on all researchers working with Laboulbeniomycetes or other understudied taxa to focus research efforts towards building solid and stable methodological, technological, and conceptual frameworks for filling knowledge shortfalls and contributing to their integration into conservation plans and policies. We present a list of research directions in the field of Laboulbeniomycetes:

1. Describing and naming new species of Laboulbeniomycetes using an integrative taxonomy approach, which means combining multiple lines of evidence supporting species delimitation.
2. Generating high-quality molecular information at both species and community levels, with the underlying objective of building a stable and well-resolved tree of life for the Laboulbeniomycetes. Key goals are (i) designing new primers specific to the class and the three orders and (ii) optimizing DNA extraction and PCR amplification protocols to enhance DNA amplification success, (iii) targeting multiple molecular markers, and (iv) generating complete genome assemblies across Laboulbeniomycetes lineages.
3. Conducting large-scale eDNA-based Laboulbeniomycetes community sampling to address their global diversity and ecological patterns across both natural and human-modified ecosystems. This necessitates the accumulation of high-quality DNA data for correctly identified Laboulbeniomycetes species in public sequence repositories to avoid interpreting the ecology of unknown and undescribed species.
4. Conducting standardized multitrophic, multiyear, and multisite monitoring programs for Laboulbeniomycetes. Standardized sampling protocols are key to building solid databases for multitrophic interaction and community ecology approaches. Similarly, standardized protocols for sampling, identifying and describing Laboulbeniomycetes species according to current scientific standards should be adopted to ensure replicable results and avoid creating knowledge ‘pipeline’ issues.
5. Screening arthropod museum collections at local and global scales for Laboulbeniomycetes ectoparasites, with a focus on host specimens representing understudied arthropod groups in undersampled geographical regions.
6. Involving citizen scientists into the multiple steps and aspects of Laboulbeniomycetes sampling campaigns, biodiversity monitoring programs, and species descriptions.
7. Leveraging the potential of new technologies (e.g., Artificial Intelligence, machine and deep learning) and techniques (e.g., high-resolution imagery such as scanning electron microscopy) in the study of Laboulbeniomycetes. For example, these could help in identifying Laboulbeniales infections based on photographs, assist researchers in daily routine informatics and analytical pipelines, and accumulate detailed basic natural history data.
8. Combining omics tools targeting RNA (transcriptomics), proteins (proteomics), and metabolism (metabolomics) in diversity and ecology-based studies focused on Laboulbeniomycetes to shed new light on their autoecology and interactions with other organisms, including the underlying ecological and evolutionary mechanisms.
9. Increasing global and local sampling efforts in poorly studied habitats that have been undersampled for Laboulbeniomycetes species, but also in already known host groups and parasite species for which type specimens have been described.

# Acknowledgments

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