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Haelewaters, Danny; Matthews, Thomas J.; Wayman, Joseph P.; Cazabonne, Jonathan; Heyman, Felix; Quandt, C. Alisha; Martin, Thomas E.
Journal of Biogeography

DOI:
10.1111/jbi. 14725

E-pub ahead of print: 23/09/2023

Publisher's PDF, also known as Version of record

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Haelewaters, D., Matthews, T. J., Wayman, J. P., Cazabonne, J., Heyman, F., Quandt, C. A., \& Martin, T. E. (2023). Biological knowledge shortfalls impede conservation efforts in poorly studied taxa-A case study of Laboulbeniomycetes. Journal of Biogeography, 51(1), 29-39. Advance online publication. https://doi.org/10.1111/jbi. 14725

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# Biological knowledge shortfalls impede conservation efforts in poorly studied taxa-A case study of Laboulbeniomycetes 

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## Funding information

U.S. National Science Foundation, Grant/ Award Number: DEB-2127291 and DEB2127290


#### Abstract

Most empirical research on biological shortfalls has focused on vertebrate taxa. This is important given many species in poorly studied groups such as invertebrates, plants, and fungi are predicted to possess high conservation risk. Here, we focus on Laboulbeniomycetes: a class of microfungi that are understudied. We examined four shortfalls: Linnean (knowledge gaps in species diversity), Wallacean (knowledge gaps in distributions), Latimerian (knowledge gaps in species persistence), and the newly introduced Scottian (knowledge gaps in species conservation assessments) shortfalls. The Linnean shortfall in Laboulbeniomycetes is hard to predict due to inconsistent species description rates. Analysis of distribution patterns indicates Laboulbeniomycetes are likely to experience an extremely high Wallacean shortfall, with many species having highly disjunct known distributions. Latimerian shortfall analysis shows over half (51\%) of Laboulbeniomycetes have not been recorded in $>50$ years, while the group has a collective Scottian shortfall of $100 \%$, given none of the 2454 described species have received an IUCN threat assessment. We suggest continued study of natural history collections, expanded citizen science programmes, and machine-learning identification approaches as important tools for reducing knowledge shortfalls in both Laboulbeniomycetes and poorly studied taxa more generally.


## KEYWORDS

fungal conservation, IUCN Red List, knowledge shortfalls, skewed specialist effect, understudied taxa

## 1 | INTRODUCTION

Numerous ecological knowledge shortfalls inhibit a full understanding of biodiversity patterns and processes (Cardoso, Erwin,
et al., 2011; Hortal et al., 2015). Many of these have a tangible impact on conservation efforts, including perhaps the two best known: the Linnean shortfall (concerning knowledge gaps of species numbers) and the Wallacean shortfall (concerning knowledge gaps of

[^1]species' geographical distributions) (Bini et al., 2006; Brito, 2010; Lomolino, 2004). Undescribed species are often overlooked in conservation prioritization and as such lack coverage from legislation to protect threatened species from overexploitation (O'Connell et al., 2020). These are important limitations given that, on average, undescribed species are predicted to be more threatened than described taxa (Liu et al., 2022). Meanwhile, a lack of knowledge of species distributions can impede understanding of priority conservation areas (Lopes-Lima et al., 2021).

Additionally, lesser-known shortfalls can inhibit conservation efforts. For example, many species have remained unobserved for many years or even decades, and the uncertain knowledge of whether such species are extant or extinct may lead to underestimates of extinction rates and inefficient allocation of conservation resources (Akçakaya et al., 2017). A new ecological shortfall relating to such 'lost' species was recently proposed (Martin et al., 2023). Named the 'Latimerian shortfall' after Marjorie Courtenay-Latimer (1907-2004), it is expressed as the number of species in a taxonomic group that are not known with certainty to be extant or extinct, based on a given threshold of the number of years since a species was last observed.

A previously undescribed shortfall is the gap between the number of species assigned a threat category on the International Union for the Conservation of Nature (IUCN) Red List (International Union for Conservation of Nature, 2022; henceforth Red List) and all known species. The Red List is a vitally important tool for conservation planning and decision-making (Rodrigues et al., 2006) although its coverage is biased, with many taxonomic groups being poorly represented (Cardoso Borges, et al., 2011; Cardoso, Erwin, et al., 2011). We propose a new shortfall to quantify gaps in the Red List coverage: the 'Scottian shortfall' after Sir Peter Markham Scott (1909-1989), cofounder of the World Wildlife Fund (later World Wide Fund for Nature), chairman of the IUCN Survival Service Commission (later Species Survival Commission), and founder of the Red List (Moore \& Rees, 2022). This shortfall can be expressed as the difference between the number of described species in a higher taxon and that of those that have been assigned an IUCN classification. Lopes-Lima et al. (2021) introduced the Ostromian shortfall that is related to the here proposed Scottian shortfall. However, while the Scottian shortfall can be quantitatively measured, the Ostromian shortfall is more vaguely defined as 'a lack of knowledge about the application and effectiveness of conservation assessments, methods, funding, and policies'.

For certain well-studied taxa, recent advances have seen several of these shortfalls substantially narrowing in recent years. For example, most bird species are now expected to have been described (Lees et al., 2020; Scheffers et al., 2012), emerging citizen science data platforms have the potential to greatly improve geographical distribution knowledge of conspicuous taxa (La Sorte \& Somveille, 2020; Mesaglio \& Callaghan, 2021), and Red List coverage continues to grow for most vertebrate groups (International Union for Conservation of Nature, 2021). However, progress has been slow with addressing knowledge shortfalls in many less conspicuous or
poorly studied taxa, including many groups of plants and most invertebrates and fungi, and the extent of these shortfalls also remains largely unquantified.

This perspective aims to explore how four shortfalls (Linnean, Wallacean, Latimerian, and Scottian) impact the conservation of a model group of poorly studied organisms: Laboulbeniomycetes, a class of fungi for which data on species diversity and distributions are available but that has never been analyzed in the context of ecological knowledge shortfalls. We explore how each of our focal shortfalls affects conservation efforts for this class (and, by extension, other poorly studied taxonomic groups) and suggest how these shortfalls can be effectively addressed in future.

## 2 | WHY LABOULBENIOMYCETES?

The class Laboulbeniomycetes (phylum Ascomycota) comprises fungi that are obligately associated with arthropods, either for dispersal purposes or as epibionts. Discovered in the 1840s, the group was put on the map by a single person who described half of the currently known diversity, Roland Thaxter (1891-1931). The class contains three orders and two unnamed clades (Blackwell et al., 2020; Goldmann \& Weir, 2018; Haelewaters, Blackwell, et al., 2021). One order, Pyxidiophorales ( 48 species in 12 genera), comprises fungi that are parasites of fungi. They produce fruiting bodies atop the hyphae of other fungi, where their sexual spores are dispersed to new fungal hosts by phoretic mites or insects (Haelewaters, Gorczak, et al., 2021). The two remaining orders, Herpomycetales (27 species in 1 genus) and Laboulbeniales ( 2370 species in 146 genera), complete their entire life cycle attached to the surface of arthropod hosts (Blackwell et al., 2020). The structures they form are miniscule (typically $250-300 \mu \mathrm{~m}$ ) and consist of a holdfast, various appendages and a fruiting body in which sexually derived spores are produced. These orders differ in developmental stages, micromorphology, and their host usage (Haelewaters et al., 2019). An additional five genera and nine species with unknown life cycle and life history are placed in two unnamed order-level clades.

A representative for other understudied groups of fungi (e.g. Blackwell, 2011; Quandt \& Haelewaters, 2021; Reynolds et al., 2022), Laboulbeniomycetes also provide an excellent case study for considering poorly studied taxonomic groups in the light of ecological knowledge shortfalls more broadly. The study of this class is impeded by their limitation to grow in artificial culture, minute size, lack of noticeability, absence of comparative traits to position them among other fungi, and melanized tissue. Even though there are some molecular protocols resulting in DNA sequences for some Laboulbeniomycetes, DNA extractions and PCR remain difficult (Haelewaters, Gorczak, et al., 2015; Sundberg et al., 2018).

Many poorly studied taxa pose similar difficulties for researchers. However, there are several reasons why this particular group offers an appropriate representative for poorly studied taxa. First, the class has a wide distribution spanning all continents except

Antarctica. It is also relatively speciose, with 2454 described species in 164 genera (Data S1). The true diversity is likely much higher, particularly given the presence of cryptic speciation in the class (Haelewaters et al., 2018, 2020). Finally, while relatively poorly studied, sufficient research into Laboulbeniomycetes has been conducted to enable analyses of a range of biological shortfalls.

## 3 | LINNEAN SHORTFALL

To generate insights into the amount of undescribed Laboulbeniomycetes richness, we plotted species or genus discovery date against cumulative number of species or genera (Figure 1; Data S2). Initially, we attempted to estimate the total number of species and genera by fitting a range of asymptotic non-linear


FIGURE 1 Patterns in Laboulbeniomycetes species discovery and taxonomic effort through time. The top row includes the discovery curves for Laboulbeniomycetes species (a) and genera (b). For (b), the date of the first species described in a genus was used as the genus discovery date. In both (a) and (b), the year a taxon was described (i.e., the publication date) was used as the discovery date. The bottom row illustrates how the number of taxonomists (log-transformed) (c) and the number of species described per taxonomist (number of described species divided by the number of taxonomists who described them) (d) have varied through time. In (c) and (d), 10-year bin widths were used, starting from the first species description in 1853. The 2013-2022 bin includes the year 2023 to avoid creating a bin containing a single year. The number of taxonomists includes all those involved in species descriptions in the 10-year intervals. In (c), a linear regression model fit (black line) to the year-log (number of taxonomists) data is shown.
regression models, including sigmoidal and convex models (Matthews et al., 2019), to the discovery curve data. However, despite providing good fits to the data (mean pseudo- $R^{2}$ values across all model fits $=0.96$ ), these model fits all produced what are likely unrealistically low estimates of total species/genus richness (Data S2). As such, these findings provide support to the idea that extrapolating discovery curves to estimate total diversity, and by extension the Linnean shortfall, are only appropriate for well-studied taxa (e.g. birds) (Bacher, 2012; Bebber et al., 2007; Stork, 2018). This underestimation is because the Laboulbeniomycetes discovery curves are not neatly monotonically and asymptotically declining curves. First, the present rate of species discovery is seemingly increasing rather than decreasing (Figure 1a). Second, there are a number of 'false plateaus', characteristic of discovery curves for understudied groups more generally (Bebber et al., 2007), where, for several decades (e.g. roughly 1930-1960 in Figure 1a), very few new species were described, followed by a rapid increase in discoveries. Had we undertaken this exercise in, say, 1950, we may have incorrectly assumed that the discovery curve had almost reached an asymptote and thus that we had effectively described all Laboulbeniomycetes. In part, this misapprehension can be attributed to the effect of one taxonomist, Thaxter, who described 1183 of currently valid species between 1891 and 1931. The presence of single specialist researchers who have periodically taken a taxonomic interest in Laboulbeniomycetes appears to exert a strong influence on both the 'false plateaus' described here and other patterns in our analysis described below; a factor we name the 'skewed specialist effect'. It is likely that a similar situation characterizes several other poorly studied groups, whereby taxonomic effort has been dominated by a handful of taxonomic experts.

It has been argued that information on the amount of taxonomic effort focused on a given taxon may also provide insights into estimating diversity and the Linnean shortfall (Costello et al., 2012; Joppa et al., 2011; Pimm et al., 2010). For all 2454 species of Laboulbeniomycetes, we sourced data on the taxonomist(s) who described the species. Using these data, we assessed how the number of taxonomists describing Laboulbeniomycetes has varied through time, using 10-year bins starting from the first species description in 1853 (2023 was included in the final bin to avoid creating a bin comprising a single year; Data S2). We found taxonomic effort to be dominated by a small number of experts, with a single individual (Thaxter) having described $48 \%$ of species in our database. Ranking taxonomists by the number of descriptions they published, the top-six taxonomists described-or were part of a team that described-approximately 2000 of the 2454 species (i.e. $>80 \%$ of species) (Figure 2).

Nonetheless, the number of taxonomists describing Laboulbeniomycetes has increased roughly exponentially over time (Figure 1c). This matches the findings of Joppa et al. (2011) for a range of mostly relatively well-studied taxa (e.g. amphibians, birds and mammals). However, Joppa et al. (2011) also observed that in most cases, the number of species described per taxonomist


FIGURE 2 Number of species descriptions per taxonomist. The six taxonomists involved with most species descriptions are shown individually, with all other 126 taxonomists grouped in the 'Others' category.
has declined since 1900 (see also Costello et al., 2012; Pimm et al., 2010). Using our sourced data on the number of Laboulbeniomycetes taxonomists, we remade the species-level discovery curve after standardizing by the number of taxonomists (i.e. dividing the number of described species by the number of taxonomists who have described species; Bacher, 2012; Pimm et al., 2010), again using 10-year bins (Figure 1d). Since approximately 1950, the number of described species per taxonomist has remained relatively constant. Thus, these findings contrast with those of Joppa et al. (2011) but match with those of Bacher (2012) for parasitic wasps, another poorly studied group. Given these results, coupled with the skewed specialist effect and the discovery process over time (Bebber et al., 2007), it is unlikely that taxonomic effort and description rates can provide reliable estimates of the Linnean shortfall for understudied groups.

How then to estimate the Linnean shortfall for Laboulbeniomycetes? An extrapolation based on fieldwork in Sulawesi estimated that there are between 15,000 and 75,000 species (Weir \& Hammond, 1997). These numbers are likely an underestimate, given that the analysis was completed in the premolecular era. Recent work has revealed a significant amount of cryptic diversity (Haelewaters et al., 2018, 2020), thus rendering the true diversity likely even higher. This is a common trend in mycology (Bickford et al., 2007; Hawksworth \& Lücking, 2017) and other organismal fields (e.g. Simkins et al., 2020). Overall, it is likely that, when dealing with groups that are understudied to such a large degree, and the only available global data being discovery dates, there will always be large uncertainty involved in estimating the Linnean shortfall. This has important conservation implications for understudied taxa given that it is very difficult to plan (and obtain funding for) effective conservation strategies (e.g. protected area network design, conservation prioritization activities) for species that have not yet been shown to exist.

## 4 | WALLACEAN SHORTFALL

To examine the Wallacean shortfall in Laboulbeniomycetes, we examined how many country records for each of the 2454 species exist in the literature beyond the original type locality (Data S3). The resulting heatmap (Figure 3) indicates that the USA has the highest reported diversity of Laboulbeniomycetes ( 376 species), with other hotspots in western Europe, Argentina, Cameroon, and Indonesia. This likely partly reflects known biases in taxonomic and survey efforts across countries that have been observed for many taxa (Hortal et al., 2015; Quandt \& Haelewaters, 2021). At the other end of the scale, $37 \%$ ( 88 countries and territories) of the countries listed in South (2017), including tropical countries such as Laos and Brunei, have zero Laboulbeniomycetes reported. Another 18\% (43 countries and territories) have just 1 or 2 species reported. Even certain 'megadiverse' countries (Mittermeier \& Mittermeier, 1997) have very little reported Laboulbeniomycetes diversity, such as Colombia (15 species) and the Democratic Republic of the Congo (17 species); this is only a fraction of the diversity reported from certain small island nations such as Grenada (53 species) and Trinidad and Tobago (93 species), or high-latitude countries such as Sweden (70 species).

This large Wallacean shortfall for Laboulbeniomycetes precludes any realistic estimate of range size for most species. This is further indicated by some striking disjunct distributions that appear in the dataset. For example, Dimorphomyces myrmedoniae was described from Guatemala but has also been reported in Spain and Ukraine. Other species of Laboulbeniomycetes that have distributions on completely different continents with no records from intervening territories include

Herpomyces chaetophilus (Mauritius, Panama, Tanzania, and USA) (Figure 3), Ilyomyces mairei (France and USA) and Laboulbenia antarctiae (Argentina, Spain, and Uruguay). Many further examples can be found in Data S1. While some of these disjunct distributions can likely be attributed to biological factors, such as introductions of host species (Haelewaters, Zhao, et al., 2015), many are the direct result of lack of study across large geographical areas. In addition, misapplication of names may have also played a factor in this observation; many species with disjunct distributions have not been sequenced and, based on the results of recent molecular phylogenetic studies (e.g. Crous et al., 2021; Haelewaters et al., 2018, 2022), it may be that some of the disjunct records may represent different, cryptic or near-cryptic species.

The Wallacean shortfall can have substantial impacts on conservation given that range size is a frequently used variable in conservation threat assessments, including the Red List (Hortal et al., 2015). Indeed, the large Wallacean shortfall observed for Laboulbeniomycetes may be a contributing factor toward the group's even larger Scottian shortfall (discussed below). Such severe disjunct distributions also preclude any accurate use of species distribution models and other similar modelling techniques, which are key tools in the conservation biogeography of rare species (Cardoso, Erwin, et al., 2011; Peterson et al., 2011).

## 5 | LATIMERIAN SHORTFALL

We determined 'last seen' dates for all 2454 species by examining all species description dates alongside more recently published


FIGURE 3 Density heat map showing the number of Laboulbeniomycetes species per country. Countries colored dark grey are those with no species records. Countries with bold borders are mega diverse countries as per Mittermeier and Mittermeier (1997). Arrowheads represent the disjunct distribution of Herpomyces chaetophilus, with records in Panama, USA (Cambridge, Massachusetts), Tanzania, and Mauritius. A single thallus of Herpomyces chaetophilus is shown, from Thaxter's (1908) original Plate XLI: fig. 14. Courtesy of the Archives of the Farlow Herbarium of Cryptogamic Botany, Harvard University.
records in Google Scholar, iNaturalist, and MyCoPortal. We used a 50-year threshold for 'lost' species (Martin et al., 2023). We found that at least $71 \%$ (1743 species) of species have no reliable observations after initial description, and the last reliable observation for $51 \%$ ( 1242 species) of species was 50 or more years ago. This is a much greater proportion than for terrestrial vertebrates (Figure 5), for which lost species represent between $1.7 \%$ and $3 \%$ of total species, depending on class (Martin et al., 2023). Additionally, while terrestrial vertebrates show a general trend of progressively fewer lost species with last seen dates in more distant time periods (Figure 4), similar patterns are not observed with Laboulbeniomycetes. Rather, most lost species in this group were last observed between 80 and 130 years ago; a time period that overlaps with the career of Thaxter, which again highlights the skewed specialist effect within poorly studied taxonomic groups.

The high Latimerian shortfall within Laboulbeniomycetes is a cause of concern with regard to conservation efforts, as it indicates that very little or no information has been published for a majority of species since their initial description. Thus, we possess no knowledge on the current status of these species, and cannot even state with confidence that all of them remain extant.

## 6 | SCOTTIAN SHORTFALL

Of the 2454 described species of Laboulbeniomycetes, none had an assessment on the Red List (International Union for Conservation of Nature, 2022) at the time of writing; the group possesses a Scottian shortfall of $100 \%$ (Figure 5). Examining our newly
coined Scottian shortfall more broadly, there is a clear difference in shortfall size between vertebrates (and particularly terrestrial vertebrates) and non-vertebrate taxa (see also Cardoso, Borges, et al., 2011; Cardoso, Erwin, et al., 2011). Comparing described diversity for birds (Handbook of the Birds of the World and BirdLife International, 2022), mammals (Mammal Diversity Database, 2022), reptiles (Uetz et al., 2022), amphibians (American Museum of Natural History, 2022), fish (Froese \& Pauly, 2022), vascular plants (Govaerts et al., 2021), Lepidoptera and Coleoptera (Stork, 2018), and fungi (Cheek et al., 2020; Index Fungorum, 2022) with their current coverage on the Red List shows very high coverage for terrestrial vertebrates (100\% for birds, $90.49 \%$ for mammals, $86.5 \%$ for reptiles, $85.8 \%$ for amphibians), $69.8 \%$ for fish, and just $6.1 \%$ for vascular plants, $1 \%$ for Lepidoptera, $0.47 \%$ for Coleoptera, and $0.4 \%$ for fungi (Figure 5). It should be noted that not all these Red List accounts are necessarily up-to-date (Miqueleiz et al., 2022) but even so, differences among taxa are dramatic. Such differences are even more striking given that they include only described diversity in these groups, with undescribed diversity in many non-vertebrate groups, including Laboulbeniomycetes, predicted to be many times greater (Hawksworth \& Lücking, 2017; Mora et al., 2011; Pimm \& Joppa, 2015; Stork, 2018).

Given that extinction risk in many of these poorly studied groups is predicted to be considerable (Cardoso, Erwin, et al., 2011; Dunn, 2005; Lughadha et al., 2020) and that IUCN assessments represent a vital tool for successful conservation outcomes (Betts et al., 2020), the severe or even complete lack of coverage in many poorly studied groups is likely to be seriously inhibiting their conservation efforts. It is likely that, on assessment, many


FIGURE 4 Line graph showing distributions of last seen dates (at the decadal scale between 50 and 199 years) for amphibians, birds, Laboulbeniomycetes, mammals, and reptiles. One reptile (Gallotia auaritae) is excluded from the graph as its last seen date is an extreme outlier in the dataset (501 years).


FIGURE 5 Bar graph showing proportions of described species in select taxa that have been assessed by the IUCN (2022). The total number of described species in each taxon follow absolute values or estimates from the following sources: Handbook of the Birds of the World and BirdLife International (2022) (birds), Mammal Diversity Database (2022) (mammals), Uetz et al. (2022) (reptiles), American Museum of Natural History (2022) (amphibians), Froese and Pauly (2022) (fish), Govaerts et al. (2021) (vascular plants), Stork (2018) (Lepidoptera, Coleoptera), Cheek et al. (2020) (fungi), and Index Fungorum (2022) (Laboulbeniomycetes).

Laboulbeniomycetes species would be classified as Data Deficient (as a comparator, currently 10.4\% of Red List-assessed fungi are classified as DD). Such assessments would, however, be more useful than a species remaining unassessed, given that DD-classifications are often indirectly indicative of threat status (e.g. Borgelt et al., 2022) and can highlight species in urgent need of further research to facilitate reclassification, in a way that unassessed species cannot (Cazalis et al., 2023).

## 7 | DISCUSSION

The first challenge in dealing with biodiversity knowledge shortfalls for a given taxon is their quantification (Hortal et al., 2015). Undertaking this task for Laboulbeniomycetes shows that biological shortfalls (i) prevent accurate modeling of overall diversity in the group, (ii) severely impede knowledge of species distributions, (iii) inhibit knowledge of whether species remain extant, and therefore (iv) preclude them receiving Red List assessments. While we have here focused on four specific shortfalls, our understanding of the ecology of, and by extension our ability to effectively conserve, Laboulbeniomycetes, is also constrained by an almost complete lack of data on their abundance (Prestonian shortfall), functional traits (Raunkiaeran shortfall), abiotic tolerances (Hutchinsonian shortfall), evolutionary relationships (Darwinian shortfall), and ecological interactions (Eltonian shortfall) (Hortal et al., 2015). These are shortcomings that are likely to apply to many other poorly studied taxonomic groups generally.

Such severe knowledge shortfalls present challenges to global conservation efforts. For example, progress towards tangible goals such as Aichi Target 12 (Convention on Biological Diversity, 2010), obtaining funding for conservation actions to preserve imperilled taxa, and raising awareness with the public and policymakers ('if you don't know it ... you won't save it'; D. Janzen in Cardoso, Erwin, et al., 2011) are hard to achieve when such taxa are not described or there are little or no data regarding where they occur, whether they are still extant, and what their predicted conservation status is. Many poorly studied groups undertake a range of essential ecosystem functions, including pollination, organic matter decomposition, nutrient recycling, biological control, and food provision (Cardoso, Erwin, et al., 2011; Noriega et al., 2018). In the case of Laboulbeniomycetes, and particularly Laboulbeniales, being parasitic, the group has substantial impacts on the regulation of their arthropod host populations, stability of food webs, and by extension ecosystem health (de Groot et al., 2020; Wang \& Wang, 2017).

Without accurate and detailed information on species numbers and distributions, Laboulbeniomycetes are unlikely to ever be considered in any protected area considerations, threat analyses, or ecosystem-based approaches to conservation; a situation that has also been recognized for insects (Chowdhury et al., 2022). It is not possible to assess how well such poorly studied groups are represented within current protected area networks, a common research exercise for vertebrates (e.g. Maiorano et al., 2015). It also becomes clear that there are different levels of poorly studied groups. A recent paper (Chowdhury et al., 2022) proposed a four-step framework to ensure insects are incorporated in future protected areas (PAs) and wider conservation efforts: (1) integrate insect conservation into management plans, (2) designate PAs explicitly for insects, (3) design wider conservation initiatives (i.e., that extend beyond PA boundaries), and (4) invest in greater monitoring and research effort for insects. However, given our analyses presented here, it is clear that, for Laboulbeniomycetes, steps 1-3 are not currently possible; the extreme data shortfalls characteristic of very understudied groups render almost all basic conservation initiatives ineffectual. Thus, a 'one-size-fits-all' approach is unlikely to be effective for the conservation of all poorly studied taxa and, for groups with severe data shortfalls, it is imperative that greater resources are put into monitoring and research efforts.

Resolving the knowledge shortfall issues described in this perspective represents a formidable challenge, given the likely diversity of poorly studied groups such as the Laboulbeniomycetes, the difficulties involved in identifying them, and the associated lack of expertise available for accurately cataloguing and monitoring such groups. Indeed, while the number of taxonomists working on Laboulbeniomycetes is seemingly increasing, numerous authors have raised general concerns regarding the pressures on taxonomy as a discipline, such as perceptions that it is academically uncompetitive, poorly funded, and (consequently) failing to attract sufficient numbers of specialists in the current generation of new scientists (Britz et al., 2020; Ebach et al., 2011; Godfray, 2002; Zeppelini et al., 2021). Furthermore, effectively addressing these shortfalls is dependent on the extensive
fieldwork necessary to locate new species, particularly in poorly sampled geographical regions (Figure 3), improve knowledge of spatial distributions, rediscover 'lost' species, and inform conservation assessments. Such targeted scientific fieldwork has also been noted to be in decline in general (Ríos-Saldaña et al., 2018), and is additionally hindered by increasingly complex requirements for research, export, and import permits (Britz et al., 2020; Neumann et al., 2018) in the case of studies examining inconspicuous organisms such as the Laboulbeniomycetes that are reliant on specimen collecting.

Emerging technologies and trends in scientific data collection may make significant contributions towards addressing knowledge gaps in poorly studied groups (Hortal et al., 2015). For example, standardized multitrophic, multiyear, and multisite monitoring programs have been proposed to build large-scale datasets to address current knowledge gaps (species distributions, abiotic tolerances, etc.) of poorly studied groups (Haelewaters, Dick, et al., 2021). In addition, citizen science may prove a powerful tool for sourcing biological data on poorly studied taxa on a scale that formal scientific surveys are not capable of (Irga et al., 2018). Similarly, arguments exist for expediting taxonomic processes by employing new approaches such as DNA metabarcoding (Kress \& Erickson, 2012) and environmental DNA analysis (Yan et al., 2018). However, these approaches have their own limitations (Cazabonne et al., 2022; de Carvalho et al., 2005). Citizen scientists are often limited in their ability to identify cryptic taxa to species-level (e.g. Kremen et al., 2011). In the case of fungi, it appears that conspicuous representatives can be effectively surveyed by citizen scientists, but observers struggle with more cryptic groups, judging from biases reported by Mesaglio and Callaghan (2021). Advances in the application of deep learning algorithms for species identification (e.g. from photographs of samples under a microscope; Chowdhury et al., 2022; Villon et al., 2020) may provide one promising avenue for data generation in groups that require expert taxonomic skills for basic taxon identification.

At its core, with certain modern scientific approaches notwithstanding, the weight of the burden for addressing biological shortfalls in poorly studied groups currently lies with specialist taxonomists, and it falls to the broader scientific community to ensure such taxonomists have the resources, infrastructure, and career stability to address these shortfalls (Britz et al., 2020; Paknia et al., 2015). Despite the challenges involved, allowing taxonomists to continue to reduce these knowledge shortfalls is vitally important for the conservation of global biodiversity. At least 1 million species are already likely to be threatened with extinction, and the vast majority of these threatened species lie within poorly studied taxa such as Laboulbeniomycetes (Barnosky et al., 2011; Díaz et al., 2019). Preventing extinctions in these groups is an acknowledged priority for the global community (Convention on Biological Diversity, 2010) but will first require a better fundamental understanding of these groups. This can only be achieved by reducing the biological knowledge shortfalls associated with them.

## ACKNOWLEDGEMENTS

No permits were required for this study. We thank Paul Kirk (Royal Botanic Garden, Kew) for downloading and sending us the species
list of Laboulbeniomycetes with holotype information. Two anonymous reviewers provided helpful and constructive comments on an earlier version of the manuscript.

## FUNDING INFORMATION

This study received support in part from the U.S. National Science Foundation (DEB-2127290 to D.H. and DEB-2127291 to C.A.Q.).

## CONFLICT OF INTEREST STATEMENT

The authors have declared no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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## REFERENCES

Akçakaya, H. R., Keith, D. A., Burgman, M., Butchart, S. H. M., Hoffmann, M., Regan, H. M., Harrison, I., \& Boakes, E. (2017). Inferring extinctions III: A cost-benefit framework for listing extinct species. Biological Conservation, 214, 336-342. https://doi.org/10.1016/j. biocon.2017.07.027
American Museum of Natural History. (2022). Amphibian species of the world 6.1, an online reference. https://amphibiansoftheworld. amnh.org/
Bacher, S. (2012). Still not enough taxonomists: Reply to Joppa et al. Trends in Ecology \& Evolution, 27, 65-66. https://doi.org/10.1016/j. tree.2011.11.003
Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., \& Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? Nature, 471, 51-57. https://doi. org/10.1038/nature09678
Bebber, D. P., Marriott, F. H. C., Gaston, K. J., Harris, S. A., \& Scotland, R. W. (2007). Predicting unknown species numbers using discovery curves. Proceedings of the Royal Society B: Biological Sciences, 274, 1651-1658. https://doi.org/10.1098/rspb.2007.0464
Betts, J., Young, R. P., Hilton-Taylor, C., Hoffmann, M., Rodríguez, J. P., Stuart, S. N., \& Milner-Gulland, E. J. (2020). A framework for evaluating the impact of the IUCN Red List of threatened species. Conservation Biology, 34, 632-643. https://doi.org/10.1111/ cobi. 13454
Bickford, D., Lohman, D. J., Sodhi, N. S., Ng, P. K. L., Meier, R., Winker, K., Ingram, K. K., \& Das, I. (2007). Cryptic species as a window on diversity and conservation. Trends in Ecology \& Evolution, 22, 148155. https://doi.org/10.1016/j.tree.2006.11.004

Bini, L. M., Diniz-Filho, J. A. F., Rangel, T. F. L. V. B., Bastos, R. P., \& Pinto, M. P. (2006). Challenging Wallacean and Linnean shortfalls: Knowledge gradients and conservation planning in a biodiversity hotspot. Diversity and Distributions, 12, 475-482. https://doi. org/10.1111/j.1366-9516.2006.00286.x
Blackwell, M. (2011). The fungi: 1, 2, 3... 5.1 million species? American Journal of Botany, 98, 426-438. https://doi.org/10.3732/ajb. 1000298

Blackwell, M., Haelewaters, D., \& Pfister, D. H. (2020). Laboulbeniomycetes: Evolution, natural history, and Thaxter's final word. Mycologia, 112, 1048-1059. https://doi.org/10.1080/00275514.2020.1718442
Borgelt, J., Dorber, M., Høiberg, M. A., \& Verones, F. (2022). More than half of data deficient species predicted to be threatened by extinction. Communications Biology, 5, 679. https://doi.org/10.1038/ s42003-022-03638-9
Brito, D. (2010). Overcoming the Linnean shortfall: Data deficiency and biological survey priorities. Basic and Applied Ecology, 11, 709-713. https://doi.org/10.1016/j.baae.2010.09.007
Britz, R., Hundsdörfer, A., \& Fritz, U. (2020). Funding, training, permitsthe three big challenges of taxonomy. Megataxa, 1, 49-52. https:// doi.org/10.11646/megataxa.1.1.10
Cardoso, P., Borges, P. A. V., Triantis, K. A., Ferrández, M. A., \& Martín, J. L. (2011). Adapting the IUCN Red List criteria for invertebrates. Biological Conservation, 144, 2432-2440. https://doi.org/10.1016/j. biocon.2011.06.020
Cardoso, P., Erwin, T. L., Borges, P. A. V., \& New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation, 144, 2647-2655. https://doi. org/10.1016/j.biocon.2011.07.024
Cazabonne, J., Bartrop, L., Dierickx, G., Gafforov, Y., Hofmann, T. A., Martin, T. E., Piepenbring, M., Rivas-Ferreiro, M., \& Haelewaters, D. (2022). Molecular-based diversity studies and field surveys are not mutually exclusive: On the importance of integrated methodologies in mycological research. Frontiers in Fungal Biology, 3, 860777. https://doi.org/10.3389/ffunb.2022.860777
Cazalis, V., Santini, L., Lucas, P. M., González-Suárez, M., Hoffmann, M., Benítez-López, A., Pacifici, M., Schipper, A. M., Böhm, M., Zizka, A., Clausnitzer, V., Meyer, C., Jung, M., Butchart, S. H. M., Cardoso, P., Mancini, G., Reşit Akçakaya, H., Young, B. E., Patoine, G., \& Di Marco, M. (2023). Prioritizing the reassessment of data deficient species on the IUCN Red List. Conservation Biology. https://doi. org/10.1111/cobi. 14139
Cheek, M., Nic Lughadha, E., Kirk, P., Lindon, H., Carretero, J., Looney, B., Douglas, B., Haelewaters, D., Gaya, E., Llewellyn, T., Ainsworth, M., Gafforov, Y., Hyde, K., Crous, P., Hughes, M., Walker, B. E., Forzza, R. C., Meng, W. K., \& Niskanen, T. (2020). New discoveries: Plants and fungi described in 2019. Plants, People, Planet, 2, 371-388. https://doi.org/10.1002/ppp3.10148
Chowdhury, S., Jennions, M. D., Zalucki, M. P., Maron, M., Watson, J. E. M., \& Fuller, R. A. (2022). Protected areas and the future of insect conservation. Trends in Ecology \& Evolution, 38, 85-95. https://doi. org/10.1016/j.tree.2022.09.004
Convention on Biological Diversity. (2010). COP 10 Decision X/2. The Strategic Plan for Biodiversity 2011-2020 and the Aichi Biodiversity Targets. https://www.cbd.int/decision/cop/?id=12268
Costello, M. J., Wilson, S., \& Houlding, B. (2012). Predicting total global species richness using rates of species description and estimates of taxonomic effort. Systematic Biology, 61, 871-883. https://doi. org/10.1093/sysbio/syr080
Crous, P. W., Osieck, E. R., Jurjevi, Ž., Boers, J., Van Iperen, A. L., StarinkWillemse, M., Dima, B., Balashov, S., Bulgakov, T. S., Johnston, P. R., Morozova, O. V., Pinruan, U., Sommai, S., Alvarado, P., Decock, C. A., Lebel, T., McMullan-Fisher, S., Moreno, G., Shivas, R. G., ... Groenewald, J. Z. (2021). Fungal planet description sheets: 1284 1382. Persoonia, 47, 178-374. https://doi.org/10.3767/persoonia. 2021.47.06
de Carvalho, M. R., Bockmann, F. A., Amorim, D. S., de Vivo, M., de Toledo-Piza, M., Menezes, N. A., de Figueiredo, J., Castro, R. M. C., Gill, A. C., McEachran, J. D., Compagno, L. J. V., Schelly, R. C., Britz, R., Lundberg, J. G., Vari, R. P., \& Nelson, G. (2005). Revisiting the taxonomic impediment. Science, 307, 353. https://doi.org/10.1126/ science.307.5708.353b
de Groot, M. D., Dumolein, I., Hiller, T., Sándor, A. D., Szentiványi, T., Schilthuizen, M., Aime, M. C., Verbeken, A., \& Haelewaters, D.
(2020). On the fly: Tritrophic associations of bats, bat flies, and fungi. Journal of Fungi, 6, 361. https://doi.org/10.3390/jof6040361 Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., ... Zayas, C. N. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (p. 56). IPBES Secretariat.
Dunn, R. R. (2005). Modern insect extinctions, the neglected majority. Conservation Biology, 19, 1030-1036. https://doi. org/10.1111/j.1523-1739.2005.00078.x
Ebach, M. C., Valdecasas, A. G., \& Wheeler, Q. D. (2011). Impediments to taxonomy and users of taxonomy: Accessibility and impact evaluation. Cladistics, 27, 550-557. https://doi.org/10.1111/j.1096-0031. 2011.00348.x

Froese, R., \& Pauly, D. (2022). FishBase ver. (08/2022). https://www. fishbase.se/search.php
Godfray, H. C. J. (2002). Challenges for taxonomy. Nature, 417, 17-19. https://doi.org/10.1038/417017a
Goldmann, L., \& Weir, A. (2018). Molecular phylogeny of the Laboulbeniomycetes (Ascomycota). Fungal Biology, 122, 87-100. https://doi.org/10.1016/j.funbio.2017.11.004
Govaerts, R., Lughadha, N. E., Black, N., Turner, R., \& Paton, A. (2021). The world checklist of vascular plants, a continuously updated resource for exploring global plant diversity. Scientific Data, 8, 215. https://doi.org/10.1038/s41597-021-00997-6
Haelewaters, D., Blackwell, M., \& Pfister, D. H. (2021). Laboulbeniomycetes: Intimate fungal associates of arthropods. Annual Review of Entomology, 66, 257-276. https://doi.org/10.1146/ annurev-ento-013020-013553
Haelewaters, D., De Kesel, A., \& Pfister, D. H. (2018). Integrative taxonomy reveals hidden species within a common fungal parasite of ladybirds. Scientific Reports, 8, 15966. https://doi.org/10.1038/s4159 8-018-34319-5
Haelewaters, D., Dick, C. W., Cocherán Pittí, K. P., Dittmar, K., \& Patterson, B. D. (2021). Chapter 21. Bats, bat flies, and fungi: Exploring uncharted waters. In B. K. Lim, M. B. Fenton, R. M. Brigham, S. Mistry, A. Kurta, E. H. Gillam, A. Russell, \& J. Ortega (Eds.), 50 years of bat research. Fascinating life sciences (pp. 349-371). Springer. https://doi.org/10.1007/978-3-030-54727-1_21
Haelewaters, D., Dima, B., Abdel-Hafiz, B. I. I., Abdel-Wahab, M. A., Abul-Ezz, S. R., Acar, I., Aguirre-Acosta, E., Aime, M. C., Aldemir, S., Ali, M., Ayala-Vásquez, O., Bakhit, M. S., Bashir, H., Battistin, E., Bendiksen, E., Castro-Rivera, R., Çolak, Ö. F., De Kesel, A., de la Fuente, J. I., ... Krisai-Greilhuber, I. (2020). Fungal systematics and evolution 6. Sydowia, 72, 231-356. https://doi.org/10.12905/0380. sydowia72-2020-0231
Haelewaters, D., Gorczak, M., Kaishian, P., De Kesel, A., \& Blackwell, M. (2021). Laboulbeniomycetes, enigmatic fungi with a turbulent taxonomic history. In Ó. Zaragoza \& A. Casadevall (Eds.), Encyclopedia of mycology (Vol. 1, pp. 263-283). Elsevier. https://doi.org/10.1016/ B978-0-12-819990-9.00049-4
Haelewaters, D., Gorczak, M., Pfliegler, W. P., Tartally, A., Tischer, M., Wrzosek, M., \& Pfister, D. H. (2015). Bringing Laboulbeniales to the 21st century: Enhanced techniques for extraction and PCR amplification of DNA from minute ectoparasitic fungi. IMA Fungus, 6, 363-372. https://doi.org/10.5598/imafungus. 2015.06.02.08

Haelewaters, D., Pfliegler, W. P., Gorczak, M., \& Pfister, D. H. (2019). Birth of an order: Comprehensive molecular phylogenetic study reveals that Herpomyces (fungi, Laboulbeniomycetes) is not part of Laboulbeniales. Molecular Phylogenetics and Evolution, 133, 286301. https://doi.org/10.1016/j.ympev.2019.01.007

Haelewaters, D., Van Caenegem, W., \& De Kesel, A. (2022). Hesperomyces harmoniae, a new name for a common ectoparasitic fungus on
the invasive alien ladybird Harmonia axyridis. Sydowia, 75, 53-74. https://doi.org/10.12905/0380.sydowia75-2022-053
Haelewaters, D., Zhao, S. Y., De Kesel, A., Royer, I. R., Handlin, R. E., Farrell, B. D., \& Pfister, D. H. (2015). Laboulbeniales (Ascomycota) of the Boston Harbor islands I: Species parasitizing Coccinellidae and Staphylinidae. Northeastern Naturalist, 22, 459-477. https:// doi.org/10.1656/045.022.0304
Handbook of the Birds of the World and BirdLife International. (2022). Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 6b. http://datazone. birdlife.org/species/taxonomy
Hawksworth, D. L., \& Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. Microbiology Spectrum, 5, FUNK-0052-2016. https://doi.org/10.1128/microbiolspec.FUNK-0052-2016
Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., \& Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. Annual Review of Ecology, Evolution, and Systematics, 46, 523-549. https://doi.org/10.1146/annurev-ecols ys-112414-054400
Index Fungorum. (2022). Search Index Fungorum. http://www.index fungorum.org/names/names.asp
International Union for Conservation of Nature. (2021). IUCN Red List 2017-2020 report. https://nc.iucnredlist.org/redlist/resou rces/files/1630480997-IUCN_RED_LIST_QUADRENNIAL_ REPORT_2017-2020.pdf
International Union for Conservation of Nature. (2022). The IUCN Red List of threatened species. Version 2022.1. https://www.iucnredlist.org/
Irga, P. J., Barker, K., \& Torpy, F. R. (2018). Conservation mycology in Australia and the potential role of citizen science. Conservation Biology, 32, 1031-1037. https://doi.org/10.1111/cobi. 13121
Joppa, L. N., Roberts, D. L., \& Pimm, S. L. (2011). The population ecology and social behaviour of taxonomists. Trends in Ecology and Evolution, 26, 551-553. https://doi.org/10.1016/j.tree.2011.07.010
Kremen, C., Ullmann, K. S., \& Thorp, R. W. (2011). Evaluating the quality of citizen-scientistdataonpollinatorcommunities.ConservationBiology, 25, 607-617. https://doi.org/10.1111/j.1523-1739.2011.01657.x
Kress, W. J., \& Erickson, D. L. (2012). DNA barcodes: Methods and protocols. Methods in Molecular Biology, 858, 3-8. https://doi. org/10.1007/978-1-61779-591-6_1
La Sorte, F. A., \& Somveille, M. (2020). Survey completeness of a global citizen-science database of bird occurrence. Ecography, 43, 34-43. https://doi.org/10.1111/ecog. 04632
Lees, A. C., Rosenberg, K. V., Ruiz-Gutierrez, V., Marsden, S., Schulenberg, T. S., \& Rodewald, A. D. (2020). A roadmap to identifying and filling shortfalls in neotropical ornithology. The Auk, 137, 1-17. https://doi. org/10.1093/auk/ukaa048
Liu, J., Slik, F., Zheng, S., \& Lindenmayer, D. B. (2022). Undescribed species have higher extinction risk than known species. Conservation Letters, 15, e12876. https://doi.org/10.1111/conl. 12876
Lomolino, M. V. (2004). Conservation biogeography. Frontiers of biogeography: New directions in the geography of nature (p. 390). Sinauer Associates.
Lopes-Lima, M., Riccardi, N., Urbanska, M., Köhler, F., Vinarski, M., Bogan, A. E., \& Sousa, R. (2021). Major shortfalls impairing knowledge and conservation of freshwater molluscs. Hydrobiologia, 848, 2831-2867. https://doi.org/10.1007/s10750-021-04622-w
Lughadha, E. N., Bachman, S. P., Leão, T. C. C., Forest, F., Halley, J. M., Moat, J., Acedo, C., Bacon, K. L., Brewer, R. F. A., Gâteblé, G., Gonçalves, S. C., Govaerts, R., Hollingsworth, P. M., KrisaiGreilhuber, I., de Lirio, E. J., Moore, P. G. P., Negrão, R., Onana, J. M., Rajaovelona, L. R., ... Walker, B. E. (2020). Extinction risk and threats to plants and fungi. Plants, People, Planet, 2, 389-408. https://doi.org/10.1002/ppp3.10146
Maiorano, L., Amori, G., Montemaggiori, A., Rondinini, C., Santini, L., Saura, S., \& Boitani, L. (2015). On how much biodiversity is covered in Europe by national protected areas and by the Natura 2000
network: Insights from terrestrial vertebrates. Conservation Biology, 29, 986-995. https://doi.org/10.1111/cobi. 12535
Mammal Diversity Database. (2022). Mammal diversity database (version 1.9.1). https://www.mammaldiversity.org/about.html
Martin, T. E., Bennett, G. C., Fairbairn, A., \& Mooers, A. O. (2023). 'Lost' taxa and their conservation implications. Animal Conservation, 26, 14-24. https://doi.org/10.1111/acv. 12788
Matthews, T. J., Triantis, K., Whittaker, R. J., \& Guilhaumon, F. (2019). Sars: An R package for fitting, evaluating and comparing speciesarea relationship models. Ecography, 42, 1446-1455. https://doi. org/10.1111/ecog. 04271
Mesaglio, T., \& Callaghan, C. T. (2021). An overview of the history, current contributions and future outlook of iNaturalist in Australia. Wildlife Research, 48, 289-303. https://doi.org/10.1071/WR20154
Miqueleiz, I., Miranda, R., Ariño, A. H., \& Cancellario, T. (2022). Effective reassessments of freshwater fish species: A case study in a Mediterranean peninsula. Hydrobiologia, 849, 1339-1349. https:// doi.org/10.1007/s10750-021-04644-4
Mittermeier, R., \& Mittermeier, C. G. (1997). Megadiversity: Earth's biologically wealthiest nations (p. 501). CEMEX.
Moore, C., \& Rees, E. C. (2022). Sir Peter Markham Scott CH. 14 September 1909-29 August 1989. Biographical Memoirs of Fellows of the Royal Society, 73, 421-443. https://doi.org/10.1098/rsbm.2022.0019
Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B., \& Worm, B. (2011). How many species are there on earth and in the ocean? PLoS Biology, 9, e1001127. https://doi.org/10.1371/journal.pbio. 1001127
Neumann, D., Borisenko, A. V., Coddington, J. A., Häuser, C. L., Butler, C. R., Casino, A., Vogel, J. C., Haszprunar, G., \& Giere, P. (2018). Global biodiversity research tied up by juridical interpretations of access and benefit sharing. Organisms, Diversity and Evolution, 18, 1-18. https://doi.org/10.1007/s13127-017-0347-1
Noriega, J. A., Hortal, J., Azcárate, F. M., Berg, M. P., Bonada, N., Briones, M. J. I., Del Toro, I., Goulson, D., Ibanez, S., Landis, D. A., Moretti, M., Potts, S. G., Slade, E. M., Stout, J. C., Ulyshen, M. D., Wackers, F. L., Woodcock, B. A., \& Santos, A. M. C. (2018). Research trends in ecosystem services provided by insects. Basic and Applied Ecology, 26, 8-23. https://doi.org/10.1016/j.baae.2017.09.006
O'Connell, D. P., Kelly, D. J., Analuddin, K., Karya, A., Marples, N. M., \& Martin, T. E. (2020). Adapt taxonomy to conservation goals. Science, 369, 1172. https://doi.org/10.1126/science.abd7717
Paknia, O., Rajaei Sh, H., \& Koch, A. (2015). Lack of well-maintained natural history collections and taxonomists in megadiverse developing countries hampers global biodiversity exploration. Organisms, Diversity and Evolution, 15, 619-629. https://doi.org/10.1007/s13127-015-0202-1
Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., MartínezMeyer, E., Nakamura, M., \& Araújo, M. B. (2011). Ecological niches and geographic distributions (p. 328). Princeton University Press. https://doi.org/10.23943/princeton/9780691136868.001.0001
Pimm, S. L., Jenkins, C. N., Joppa, L. N., Roberts, D. L., \& Russell, G. J. (2010). How many endangered species remain to be discovered in Brazil? Nature Conservation, 8, 71-77. https://doi.org/10.4322/ natcon. 00801011
Pimm, S. L., \& Joppa, L. N. (2015). How many plant species are there, where are they, and at what rate are they going extinct? Annals of the Missouri Botanical Garden, 100, 170-176. https://doi. org/10.3417/2012018
Quandt, C. A., \& Haelewaters, D. (2021). Phylogenetic advances in Leotiomycetes, an understudied clade of taxonomically and ecologically diverse fungi. In Ó. Zaragoza \& A. Casadevall (Eds.), Encyclopedia of mycology (Vol. 1, pp. 284-294). Elsevier. https://doi. org/10.1016/B978-0-12-819990-9.00052-4
Reynolds, N. K., Jusino, M. A., Stajich, J. E., \& Smith, M. E. (2022). Understudied, underrepresented, and unknown: Methodological biases that limit detection of early diverging fungi from environmental samples. Molecular Ecology Resources, 22, 1065-1085. https://doi.org/10.1111/1755-0998.13540

Ríos-Saldaña, C. A., Delibes-Mateos, M., \& Ferreira, C. C. (2018). Are fieldwork studies being relegated to second place in conservation science? Global Ecology and Conservation, 14, e00389. https://doi. org/10.1016/j.gecco.2018.e00389
Rodrigues, A. S. L., Pilgrim, J. D., Lamoreux, J. F., Hoffmann, M., \& Brooks, T. M. (2006). The value of the IUCN Red List for conservation. Trends in Ecology \& Evolution, 21, 71-76. https://doi.org/10.1016/j. tree.2005.10.010
Scheffers, B. R., Joppa, L. N., Pimm, S. N., \& Laurance, W. F. (2012). What we know and don't know about Earth's missing biodiversity. Trends in Ecology \& Evolution, 27, 501-510. https://doi.org/10.1016/j. tree.2012.05.008
Simkins, A. T., Buchanan, G. M., Davies, R. G., \& Donald, P. F. (2020) The implications for conservation of a major taxonomic revision of the world's birds. Animal Conservation, 23, 345-352. https://doi. org/10.1111/acv. 12545
South, A. (2017). Rnaturalearth: World map data from natural earth. R package version 0.1.0. https://github.com/ropenscilabs/rnaturalearth
Stork, N. E. (2018). How many species of insects and other terrestrial arthropods are there on earth? Annual Review of Entomology, 63, 31-45. https://doi.org/10.1146/annurev-ento-020117-043348
Sundberg, H., Ekman, S., \& Kruys, Å. (2018). A crush on small fungi: An efficient and quick method for obtaining DNA from minute ascomycetes. Methods in Ecology and Evolution, 9, 148-158. https://doi. org/10.1111/2041-210X. 12850
Thaxter, R. (1908). Contribution toward a monograph of the Laboulbeniaceae: Part II. Memoirs of the American Academy of Arts and Sciences, 13, 219-469. https://doi.org/10.2307/25058090
Uetz, P., Freed, P., Aguilar, R., \& Hošek, J. (2022). The reptile database. http://www.reptile-database.org
Villon, S., Mouillot, D., Chaumont, M., Subsol, G., Claverie, T., \& Villéger, S. (2020). A new method to control error rates in automated species identification with deep learning algorithms. Scientific Reports, 10, 10972. https://doi.org/10.1038/s41598-020-67573-7

Wang, C., \& Wang, S. (2017). Insect pathogenic fungi: Genomics, molecular interactions, and genetic improvements. Annual Review of Entomology, 62, 73-90. https://doi.org/10.1146/annurev-ento-031616-035509
Weir, A., \& Hammond, P. M. (1997). Laboulbeniales on beetles: Host utilization patterns and species richness of the parasites. Biodiversity and Conservation, 6, 701-719. https://doi.org/10.1023/A:10183 18320019
Yan, D., Mills, J. G., Gellie, N. J., Bissett, A., Lowe, A. J., \& Breed, M. F. (2018). High-throughput eDNA monitoring of fungi to track functional recovery in ecological restoration. Biological Conservation, 217, 113-120. https://doi.org/10.1016/j.biocon.2017.10.035
Zeppelini, D., Molin, A. D., Lamas, C. J. E., Sarmiento, C., Rheims, C. A., Fernandes, D. R. R., Lima, E. F. B., Silva, E. N., Carvalho-Filho, F., Kováč, L., Montoya-Lerma, J., Moldovan, O. T., Souza-Dias, P. G. B., Demite, P. R., Feitosa, R. M., Boyer, S. L., Weiner, W. M., \& Rodrigues, W. C. (2021). The dilemma of self-citation in taxonomy. Nature Ecology \& Evolution, 5, 2. https://doi.org/10.1038/s41559-020-01359-y

## BIOSKETCH

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Author contributions: Danny Haelewaters, Thomas J. Matthews, and Thomas E. Martin were involved in conceptualization. Thomas J. Matthews and Thomas E. Martin were involved in software. Danny Haelewaters, Thomas J. Matthews, Joseph P. Wayman, Jonathan Cazabonne, Felix Heyman, C. Alisha Quandt, and Thomas E. Martin were involved in formal analysis. Danny Haelewaters was involved in data curation. Thomas J. Matthews and Thomas E. Martin were involved in visualization. Danny Haelewaters, Thomas J. Matthews, and Thomas E. Martin were involved in writing-original draft. Danny Haelewaters, Thomas J. Matthews, C. Alisha Quandt, and Thomas E. Martin were involved in writing-review \& editing. Danny Haelewaters and Thomas E. Martin were involved in supervision.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Haelewaters, D., Matthews, T. J., Wayman, J. P., Cazabonne, J., Heyman, F., Quandt, C. A., \& Martin, T. E. (2024). Biological knowledge shortfalls impede conservation efforts in poorly studied taxa-A case study of Laboulbeniomycetes. Journal of Biogeography, 51, 29-39. https://doi.org/10.1111/jbi. 14725


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