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What Do the First 597 Global Fungal Red List Assessments Tell Us about the Threat Status of Fungi?

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Abstract: Fungal species are not immune to the threats facing animals and plants and are thus also prone to extinction. Yet, until 2015, fungi were nearly absent on the IUCN Red List. Recent efforts to identify fungal species under threat have significantly increased the number of published fungal assessments. The 597 species of fungi published in the 2022-1 IUCN Red List update (21 July 2022) are the basis for the first global review of the extinction risk of fungi and the threats they face. Nearly 50% of the assessed species are threatened, with 10% NT and 9% DD. For regions with a larger number of assessments (i.e., Europe, North America, and South America), subanalyses are provided. Data for lichenized and nonlichenized fungi are also summarized separately. Habitat loss/degradation followed by climate change, invasive species, and pollution are the primary identified threats. Bias in the data is discussed along with knowledge gaps. Suggested actions to address these gaps are provided along with a discussion of the use of assessments to facilitate on-the-ground conservation efforts. A research agenda for conservation mycology to assist in the assessment process and implementation of effective species/habitat management is presented.

Keywords: conservation; threats; Basidiomycota; Ascomycota; lichens; funga; IUCN; extinction risk

1. Introduction

Fungi are heterotrophic organisms with astonishing morphological and physiological variety. They are among the most diverse group of organisms on Earth [1–3] and are involved in a myriad of associations with the environment and other living beings. Fungi are vital in ecosystem maintenance through nutrient cycling and symbiosis with other organisms, such as mycorrhizal and endophytic fungi, as well other indirect associations that enhance plant productivity and resilience to environmental stress [4]. Humans also benefit directly from fungi, from food to drug production, including recent advances in clothing and construction [5,6]. Despite their importance, fungi are among the most understudied organisms, with only approximately 5% of the estimated 2.2–3.8 million species described so far [3,7,8].

The lack of basic knowledge regarding the biodiversity of fungi is extremely concerning in a changing world. It is widely accepted that we are living in the Anthropocene, a period in which human actions are effectively changing the biological and chemical systems of the Earth [9]. There are multiple drivers of biodiversity loss including deforestation, reduction of habitat quality, invasive species, overexploitation, climate change, and a weak framework of political governance [10,11]. The negative effects of biodiversity loss on humanity have been well documented, both through interruptions in ecosystem functions and services [12,13] and directly on human health (such as the COVID-19 pandemic [14]). It has also been argued that we are facing the sixth mass extinction, the first one caused by human action instead of natural events [15].

Fungal species are not immune to the threats facing animals and plants and are thus also prone to extinction [16]. Fungi occur in all habitats throughout the world, with the composition and distribution of communities of species correlated with environmental and biotic factors such as climate, water and soil chemistry, distance from the equator, animals and plant community composition, presence/existence of symbionts, and habitat quality [17,18]. Thus, disturbances in these factors can negatively affect the distribution and population size of fungal species, eventually rendering them at risk of extinction.

The IUCN (International Union for Conservation of Nature) Red List of Threatened Species™ (henceforth Red List) is a global list of species and their conservation status, along with associated information regarding species distribution, habitat, ecology, population size, trends, structure, threats, and conservation [19]. The Red List is an important resource to support concrete conservation policy, planning, and action. It helps authorities delimit protected areas, guides funding allocation and influences development decisions [20]. It has also been used as an indicator to measure and monitor the state of global biodiversity for different global framework targets, such as Aichi Target 12 and Sustainable Development

Goal 15, and will likely be used for the Post-2020 Global Biodiversity Framework [21–23]. The Red List is divided into categories according to the degree of threat to which a species is subject. The categories range from Least Concern (LC) to Extinct (EX), with three "threatened" categories: Vulnerable (VU), Endangered (EN), and Critically Endangered (CR), in addition to a Near Threatened category (NT). The Data Deficient (DD) category includes species for which there is not enough information to make an assessment of their extinction risk [19]. The assessment of the degree of threat is carried out using five defined criteria that can be routinely applied. The criteria (A-E and their subcriteria) are based on population size, structure, and trends as well as geographic distribution, allowing for comparison and reproducibility across taxonomic groups [19].

The Red List was initiated in 1964, but the first fungal species (two species of lichenized fungi, *Cladonia perforata* A. Evans and *Erioderma pedicellatum* (Hue) P.M.Jørg.) were included only in 2003 [24], with *Pleurotus nebrodensis* (Inzenga) Quél. ssp. *nebrodensis* added in 2006. Additional fungal species were not added until 2014, and fungi remain one of the most underrepresented kingdoms on the Red List. The 50 year delay in efforts to globally assess the conservation status of fungi was due both to the paucity of taxonomic, ecological, and distributional data and an initial misconception that a rigorous assessment of the conservation status of fungi was not feasible due to the fact of their unique biology [7,16]. Essential concepts such as the number of mature individuals and generation length, used for applying the assessment criteria, are difficult to calculate for fungi. Dahlberg and Mueller [16] addressed this in 2011 by providing suggested operational methods and definitions along with clear examples of how to interpret these concepts for fungal red listing that are applicable to most fungal groups. It is therefore possible to infer the threat status of fungi and to understand trends based on the analysis of our increasing knowledge of fungal diversity and distribution, their ecology, and the status and trends in their habitats [20].

There is more information regarding threatened fungi at the national level. Efforts began in the 1980s in Europe, and by 1992, 11 countries had national lists [25]. Currently approximately 40 countries have national Red Lists with over 10,000 species assessed and listed (e.g., see the national lists cited in [25,26]). Some national lists strictly apply the IUCN Red List criteria while others use different systems. There is also variation in the governance of national lists, with only some established under formal legislation. Nevertheless, the threat assessment process for national lists usually includes information on the population's features and threats that would assist assessments under the IUCN criteria. Therefore, the species on these national lists are often the initial focus of global conservation assessments.

The Global Fungal Red List Initiative (GFRLI) was started in 2013 [27], with the first workshops focused on assessing species of fungi at the global level commencing soon after. The workshops have proven to be instrumental in mobilizing networks of mycologists in the gathering of data and discussing, writing, reviewing, and publishing assessments. Workshops have typically been focused on specific regions and may also focus on specific taxa. A key part of the workshops has been Red List training. Participants manage data and draft assessments through the GFRLI website (http://iucn.ekoo.se/). The GFRLI platform facilitates in-depth discussions during workshops but also allows for draft assessments to be publicly viewable and commented upon by other mycologists anywhere in the world. At the end of each workshop, a set of assessments is ready for submission to the Red List Unit.

The first workshop took place in February 2015 (Sweden) and was followed by 16 additional workshops, the most recent in 2021. Thirteen of these have dealt with macrofungi, five with lichenized fungi, and one focused on rust and smut fungi. Three of these workshops had global focus, while the others were regionally focused (see events and workshops at: http://iucn.ekoo.se/). These workshops have served to develop local capacities, such as in South America, where the mycological community of several countries is actively working to evaluate species and develop projects for the conservation of fungi. Each workshop was organized under the auspices and with the help of one of the five taxon-focused specialist groups that were established within the IUCN Species Survival Committee in 2009 (https://www.iucn-fungi.org/training-and-workshop).

Assessed species have largely been selected by the participants, mainly those suspected to be of conservation interest, have sufficient information for assessment, and those in which participants have knowledge and interest. In addition, three other initiatives have taken place within the GFRLI: (1) the edible mushrooms initiative, resulting in 35 species assessed; (2) chanterelles, with the ongoing aim of assessing all chanterelles; (3) an ongoing assessment focused on the fungi of western North America. These focused assessment projects are providing a more balanced view of the threat status of groups of fungi compared to the set of species assessed during workshops that were selected a priori as potentially threatened.

The 597 species of fungi published in the 2022-1 Red List update (21 July 2022) are the basis for this first global review of the extinction risk of fungi and the threats they face. For regions with a larger number of assessments (i.e., Europe, North America, and South America), subanalyses are provided. Data for lichenized and nonlichenized fungi are also summarized separately. Bias among the assessed species is discussed along with knowledge gaps. We conclude with a discussion of the management of threatened fungi and prospects for future advancements in threat listing and in the conservation of fungi.

2. Materials and Methods

Information on listed species was downloaded from the IUCN Red List of Threatened Species, version 2022-1 [24]. In rare cases where errors were identified in the published assessment, we updated our dataset based on the authors' knowledge (e.g., one species had fishing as a threat in error). Analyses were undertaken at the species level, as the only published global assessment at a lower taxonomy level was for *Pleurotus nebrodensis* ssp. *nebrodensis*.

Species were assigned to ecological guilds coded as mutualism-ectomycorrhizal, mutualism-lichenized, parasite on fungi, parasite on insects, parasite on plants, saprotroph (indicated as saprotroph-dung, saprotroph-soil, or saprotroph-wood, where known), and unknown. This assignment was based on documentation in the assessments, complemented with information retrieved from FunGuild [28] using an API connection within a custom Python 3.9.7 script [29] and then manually checked for each species based on the authors' knowledge. Species were also assigned to simplified growth forms, with the categories lichens, macrofungi, and microfungi. Macrofungi were further divided into those with fleshy and tough sporing bodies. Where lichenized fungi (both a trophic guild and a growth form) were analyzed separately; they are referred to as lichens.

Threats were analyzed for species assessed at a threat category of near threatened (NT) or higher at the highest level based on the IUCN-CMP Unified Classification of Direct Threats (https://www.iucnredlist.org/resources/threat-classification-scheme). However, for some threats, it was pertinent to split them further (e.g., biological resource use was split into logging and collecting, and natural systems modifications was split into fire and fire suppression and dams and water management/use, while other ecosystems modifications were lumped with "other threats"). The compiled list was qualitative, not quantitative, and it did not provide an estimate of actual relative importance of different threats due to the small sample size, biases in species sampled, and the fact that most assessments list more than one threat without indicating the relative importance.

Data treatment and visualization were performed in R 4.2.0 [30] using the ggplot2 package 3.3.6 [31], ComplexUpset 1.3.3 [32] and, when necessary, figures were finalized in GIMP 2.10 [33].

3. Results

3.1. Assessed Species over Time

As of 21 July 2022, 597 species of fungi are included in the Red List (e.g., Figure 1, Box 1). The first fungal species were added to the Red List in 2003 (two lichenized species), but it was not until 2015 that efforts began to accelerate, with most species added in the last three years (Figure 2).

Figure 1. Remarkable fungal species assessed in the IUCN Red List: (**a**) *Lepraria lanata* Tønsberg assessed as EN (photo by James Lendemer); (**b**) *Fomitiporia nubicola* Alves-Silva, Bittencourt & Drechsler-Santos assessed as VU (photo by G. Alves-Silva); (**c**) *Cortinarius crypticus* (E. Horak) Soop & B. Oertel assessed as DD (photo by Ross Beever, Manaaki Whenua); (**d**) *Clavaria zollingeri* Lév. assessed as VU (photo by Michael Krikorev); (**e**) *Suillus luteus* (L.) Roussel assessed as LC (photo by Michael Krikorev); (**f**) *Hypocreopsis amplectens* T.W. May & P.R. Johnst. assessed as CR (photo by Tom May); (**g**) *Rubroboletus dupainii* (Boud.) Kuan Zhao & Zhu L. Yang assessed as NT (photo by Vladimír Kunca); (**h**) *Phallus aureolatus* L. Trierveiler-Pereira & A.A.R. de Meijer assessed as VU (photo by J.M. Baltazar); **(i)** *Mobergia calculiformis* (W.A. Weber) H. Mayrhofer & Sheard assessed as EN (photo by Frank Bungartz).

Box 1. Examples of fungi included in the IUCN Red List (see also Figure 1). Information taken and adapted from the Red List assessments [24].

***Hypocreopsis amplectens*—Tea-tree Fingers** **Critically Endangered**

Hypocreopsis amplectens forms finger-like sporing bodies as a parasite of another fungus, which decays woody branches that are small in diameter. It is known from very few sites in southern Australia and only two sites in New Zealand. It has been a target species of a long-running citizen science fungi mapping scheme that has yielded few records over several decades of monitoring. Even allowing for undetected populations, the global population is estimated as likely to be no more than 200 individuals. Most sites in southern Australia are threatened by sand-mining, which has significantly reduced the available habitat. While fire is an integral part of much of the habitat of *H. amplectens*, its survival relies on a patchwork of burnt and unburnt vegetation to allow recolonization after fire, as the fungus does not have a known resting stage and the substrate is totally consumed by fire. Therefore, an additional risk is the increase in the frequency and extent of wildfires caused by climate change. With a small population size, low numbers of individuals in each subpopulation, and ongoing habitat decline resulting in a continuing decline in population size, *H. amplectens* is assessed as Critically Endangered under the C criterion (C2a(i)).

***Lepraria lanata*—Appalachian Dust Bunnies** **Endangered**

Lepraria lanata is a crustose lichen that forms fluffy, cotton-like balls of fungi and algae that rest on a cushion of fungal tissue. It grows directly on rocks at high elevations and is endemic to the southern

Appalachian Mountains in eastern North America. Thorough and directed searches for *L. lanata* throughout the Appalachian Mountains have solidified knowledge of the species' distribution, facilitated estimations of the population size, and provided foundational data for species distribution modeling and projection under multiple climate change scenarios. Major past and ongoing threats to this species include logging and habitat alteration due to the fact of invasive species killing dominant tree species that provide essential shade as well as climate change leading to hotter and drier conditions in addition to elevating the cloud layer that often engulfs the species' habitat. *Lepraria lanata* is dependent on cool, wet environments and, therefore, hotter, drier, and more exposed conditions are likely to cause substantial declines in the population. Essential conservation actions include protecting all populations of the species and developing translocation and transplantation methods. Past habitat decline due to the fact of logging and the impact of invasive species resulted in an assessment as Endangered under the A criterion (A2ce).

Fomitiporia nubicola **Vulnerable**

Fomitiporia nubicola is a wood-inhabiting perennial polypore found exclusively on living or dead *Drimys angustifolia* (Winteraceae). The host is a relictual and endemic tree of cloud forests in southern Brazil with high ecological importance, and it is expected that *F. nubicola* follows the distribution of its host. Cloud forests in southern Brazil are threatened by climate changes and human activities, such as cattle grazing, alien species, fire, and land use changes, resulting in ongoing declines of this habitat, even in protected areas. Because the population is estimated at no more than 10,000 individuals across no more than 100 sites in one single subpopulation, the projected declines resulted in an assessment as Vulnerable under the C criterion (C2a(ii)). Conservation actions for the species include protection of known habitat and surveys to better understand the species' distribution. Following the assessment, a project was carried out to investigate the distribution of the fungus. *Fomitiporia nubicola* was not found elsewhere; additionally, it seemed to be extinct in one of the two previously known sites, with no specimens resampled. Therefore, when the status is next re-assessed, it is likely that this species will switch from Vulnerable to a higher threat category.

***Suillus luteus*—Slippery Jack** **Least Concern**

Suillus luteus is a common ectomycorrhizal mushroom in coniferous forests associated with two-needle pine trees (*Pinus* spp.) on sandy and acid soil. It is commonly found all over the Northern Hemisphere and is native to Eurasia. It was widely introduced by way of pine plantations around the globe including South America, Africa, Australia, and New Zealand. It is edible and sought after in some parts of the world, especially in regions that do not have extensive native ectotrophic forests that produce abundant large edible fungi. Its population is stable to increasing. The species can fruit prolifically, and harvest pressure is not a threat. It was assessed as Least Concern (LC).

Cortinarius crypticus **Data Deficient**

Cortinarius crypticus is a species endemic to New Zealand, restricted to the alpine South Island. It associates with beech (Nothofagaceae) as an ectomycorrhizal partner. It is known from three collections, each from a separate site, recorded between 1968 and 2004. The detectability of this species is relatively low, and it has probably been overlooked. It has a broad potential range because of the wide-spread mycorrhizal host. The apparently limited distribution and population may be due to the potential loss of dispersal vectors (i.e., native animals) resulting in a historic and continued decline. Sufficient data are lacking to enable estimations of its distribution and population size and trends. It was assessed as Data Deficient (DD).

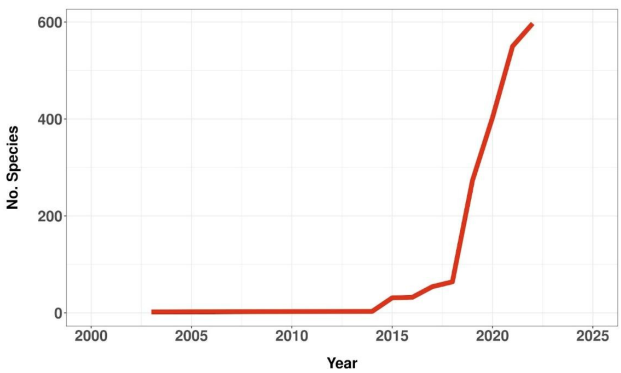


Figure 2. Accumulated number of fungi species published on the Red List since the first two lichens were assessed in 2003.

3.2. Red List Categories and Declines

A total of 345 (58%) assessed fungal species are listed at a threat category or NT [24] of which 284 (48%) are threatened (Figure 3). Among these, 32 (5%) are CR, 101 (17%) are EN, 151 (25%) are VU, and 61 (10%) are NT. The remaining published species are listed as DD (52, 9%) or LC (200, 34%).

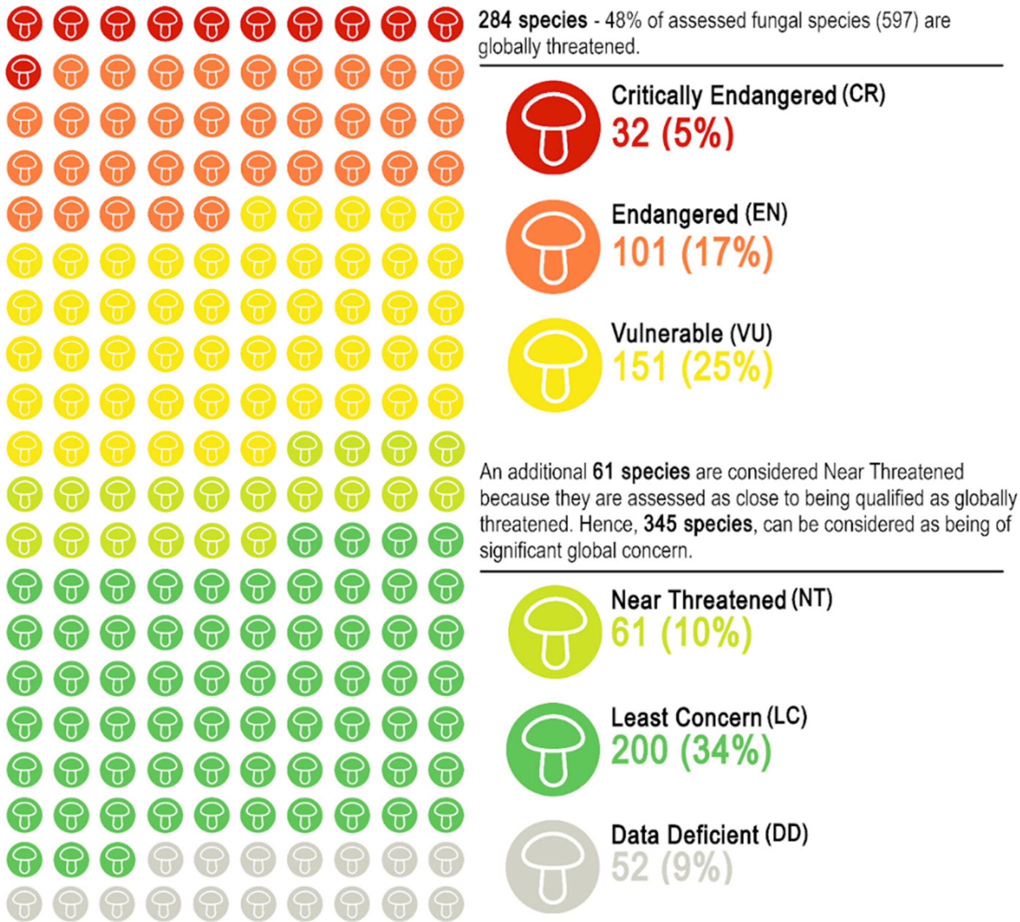


Figure 3. Number of species at different Red List categories for the 597 fungi currently globally assessed on the IUCN Red List (July 2022). Refer to the text for bias on species selection and why the proportion of Red List categories is not globally representative of fungi in general.

Overall, population trends were indicated as declining for approximately half of the species. The population of most species listed as threatened or NT were reported as declining, e.g., in 66% of CR species and 89% of NT species. Population trends were unknown for 20% of the species including 94% of the DD species.

3.3. Application of the Red List Criteria in Assessments of Fungi

In the assessments of threatened fungi, four of the five criteria (i.e., A, B, C, and D) were utilized across 284 assessments (Figure 4). No fungi were assessed under criterion E (i.e., quantitative analysis). Criteria A (i.e., population size reduction) and C (i.e., small population size and decline) were the most commonly applied criteria (92 and 116 species, respectively). Criteria B (i.e., geographic range and fragmentation, decline, and/or extreme fluctuations) and D (i.e., very small or restricted population) were also utilized (70 and 65 species, respectively). Most species were assessed under a single criterion, but some (18%) were assessed using various combinations of all four criteria, most often B + C (13).

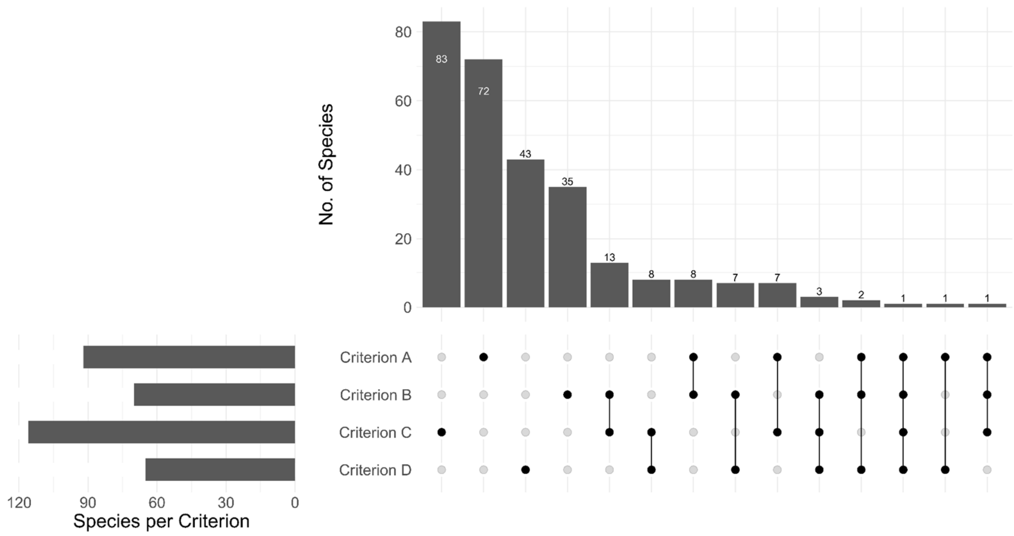


Figure 4. Criteria used in global assessments of threatened fungi in the Red List (n = 284) showing the frequency with which individual criterion (dots) and combinations of criteria (dots joined by vertical lines) were utilized. Criterion A is related to population size reduction, criterion B to restricted geographic range, criterion C to small population size and decline, and criterion D to very small or restricted population and distribution range.

3.4. Taxonomy and Growth Form

Among the species of fungi on the Red List, all are either Basidiomycota (468, including one lichenized species) or Ascomycota (129, including 93 lichenized species) (Figure 5). At the class level, most (92%) are Agaricomycetes (465) or Lecanoromycetes (85, all of which are lichenized).

In total, there are 94 lichens (16%). The most prevalent growth form among other species, representing more than half of all species (62%), is Basidiomycota-fleshy macrofungi (372) of which most are agarics (228) or boletes (67). The other growth forms are Ascomycota-fleshy macrofungi (28), Ascomycota-tough macrofungi (10), Basidiomycota-microfungus (3, all of which are smut fungi), and Basidiomycota-tough macrofungi (90), with the most prevalent being polypores (45).

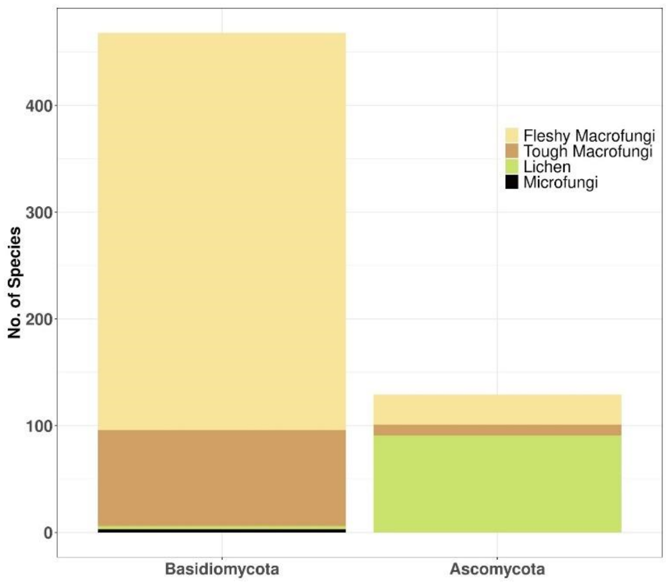


Figure 5. Number of species assessed on the Red List according to growth form among two taxonomic groups: Basidiomycota and Ascomycota (n = 597).

3.5. Trophic Guild

In terms of trophic guild, nearly half (46%) of the assessed species are mutualism-ectomycorrhizal (276) (Figure 6a). Other trophic guilds are saprotroph (174), most often not specified to substrata (99) or on wood (52); mutualism-lichenized (93); parasite (20), mostly on plants (11). The trophic guild is unknown for 6% of species (34), most of which are threatened (88%) (Table 1).

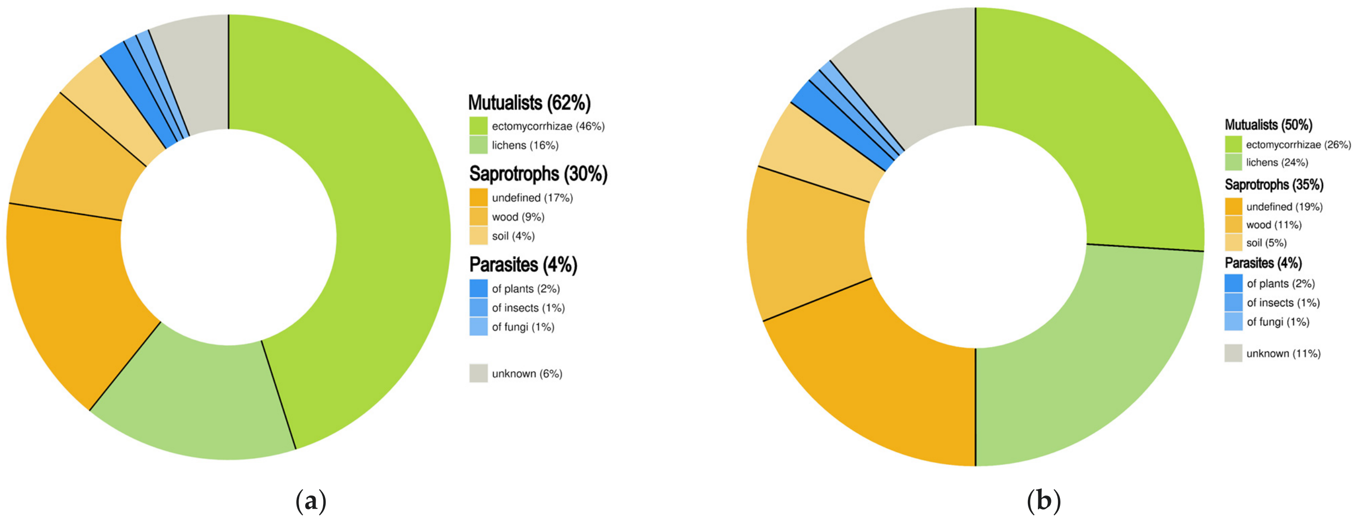


Figure 6. Proportion of different trophic guilds for (**a**) all assessed fungi (n = 597) and (**b**) threatened species in the July 2022 Red List update (n = 284).

Table 1. Number of assessed and threatened species from each trophic mode.

Trophic Mode	Number of Assessed Species	Number of Threatened Species
Mutualists	369	143
Parasites	20	11
Saprotrophs	174	100
Unknown	34	30

A similar pattern was found when considering only threatened species, with most being mutualism-ectomycorrhizal (74, 106 if NT species are included), followed by mutualism-lichenized (69, 70 including NT), saprotroph without specified substrata (54, 72 including NT), sapotroph on wood (32, 39 including NT), and trophic guild unknown (30, 33 including NT) (Figure 6b).

3.6. Geography and Habitats

Most assessed and threatened fungi on the Red List are found in forests (Figures 7 and 8). The other common habitats for both assessed and threatened species are grassland and shrubland for nonlichenized Basidiomycota and Ascomycota and rocky, shrubland, and marine/coastal habitats for threatened lichens.

In terms of realms, the greatest number occur in the Nearctic and Palaearctic areas (273 and 184 species, respectively) with 170 species having Neotropical distribution (Figure 9). Comparatively few species have been assessed from the Afrotropical (14), Indomalayan (22), Australasian (76), and Oceanian (6) realms.

Species assessed as DD mainly occur in Neotropical and Nearctic areas. Concentrations of threatened fungi (CR, EN and VU) are mostly in Neotropical (82 species), Nearctic (82), and Palearctic (96) regions (Figure 9), where most assessments have been completed. Large areas, such as the Antarctic, Oceanian, Afrotropical, and Indo-Malayan regions, are undersampled and underassessed, resulting in less than 20% of the total assessed species.

Among ectomycorrhizal fungi, 124 assessed species are in the Nearctic region, 73 in the Palearctic, and 65 in the Neotropics. Most species have been categorized as LC (97) and DD (13) in the Nearctic. In the Palearctic, LC, NT, and VU species are represented. In the Neotropics, DD, LC, and VU are the most important categories. Among the 99 species of saprotrophs evaluated, nearly one-third correspond to species distributed in the Neotropics (37), Palearctic (30), and Nearctic (29). For this guild, the categories LC, NT, and VU are the most common. Another group that has been actively included in the Red List are lichens, mainly from the Nearctic (69 species), where the most common categories are LC, EN, and CR, similar to what was found in the Palearctic (20 species). For the Neotropics (20 species), the main categories are LC and VU.

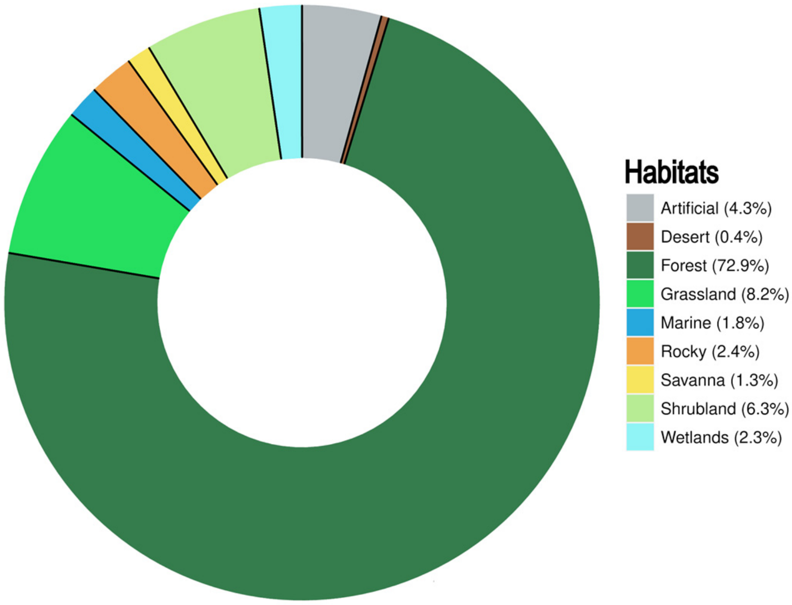


Figure 7. Proportion of assessed fungi species in the different main habitats. Note that species may be present in more than one habitat.

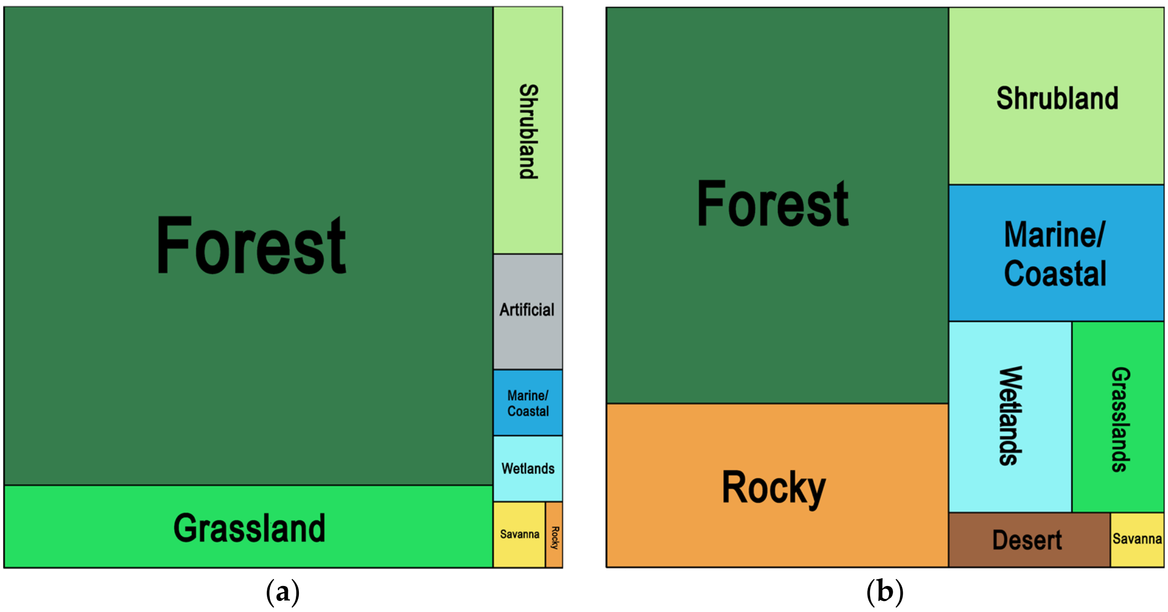
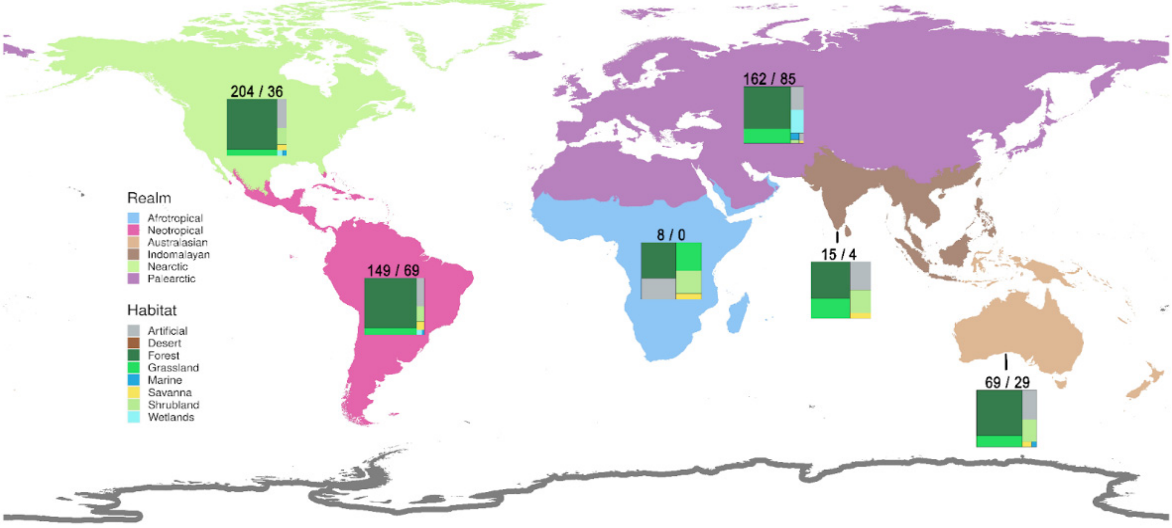
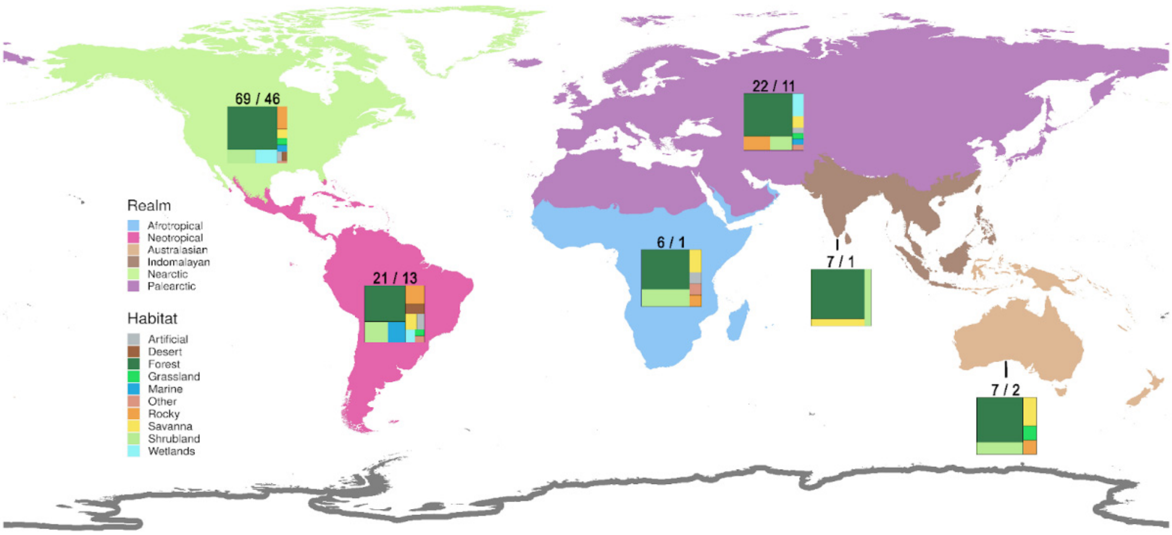


Figure 8. Proportion of threatened (**a**) nonlichenized fungi (n = 272) and (**b**) lichens (n = 106) in the different main habitats. Note that species may be present in more than one habitat.



(**a**)



(**b**)

Figure 9. Number of assessed species/threatened species in different biogeographic realms for (**a**) nonlichenized fungi and (**b**) lichens. The boxes illustrate the corresponding habitat occupied by these species. Note that species may be present in more than one habitat. Oceania and Antarctica were excluded from the maps.

3.7. Threats

The most frequently listed threats to threatened and NT species were residential and commercial development (178 species) followed by agriculture (161) and logging (157) (Figure 10A).

When considering the growth form, these listed threats remain in the top three for nonlichenized Basidiomycota and Ascomycota, although for Ascomycota, logging is the second most common and agriculture the third (Figure 10B). In contrast, for lichens, the top three listed threats are climate change (47 species), residential and commercial development (34), and human disturbance (26) (Figure 10C). There are also further listed threats that apply to a significant proportion of lichen species including logging (25 species), fire/fire suppression (24), invasives (23), pollution (22), and agriculture (21).

When considering the trophic guild, the listed threats for lichens are the same as for the growth form (see above). For ectomycorrhizal fungi, the top three listed threats are logging (69 species), residential and commercial development (61), and agriculture (37). For saprotrophs, the most frequently listed threat is agriculture (72 species), the second is logging (56 species), and the third is fire and fire suppression (55 species) (residential and commercial is fourth (54 species), although only 2 species lower than logging).

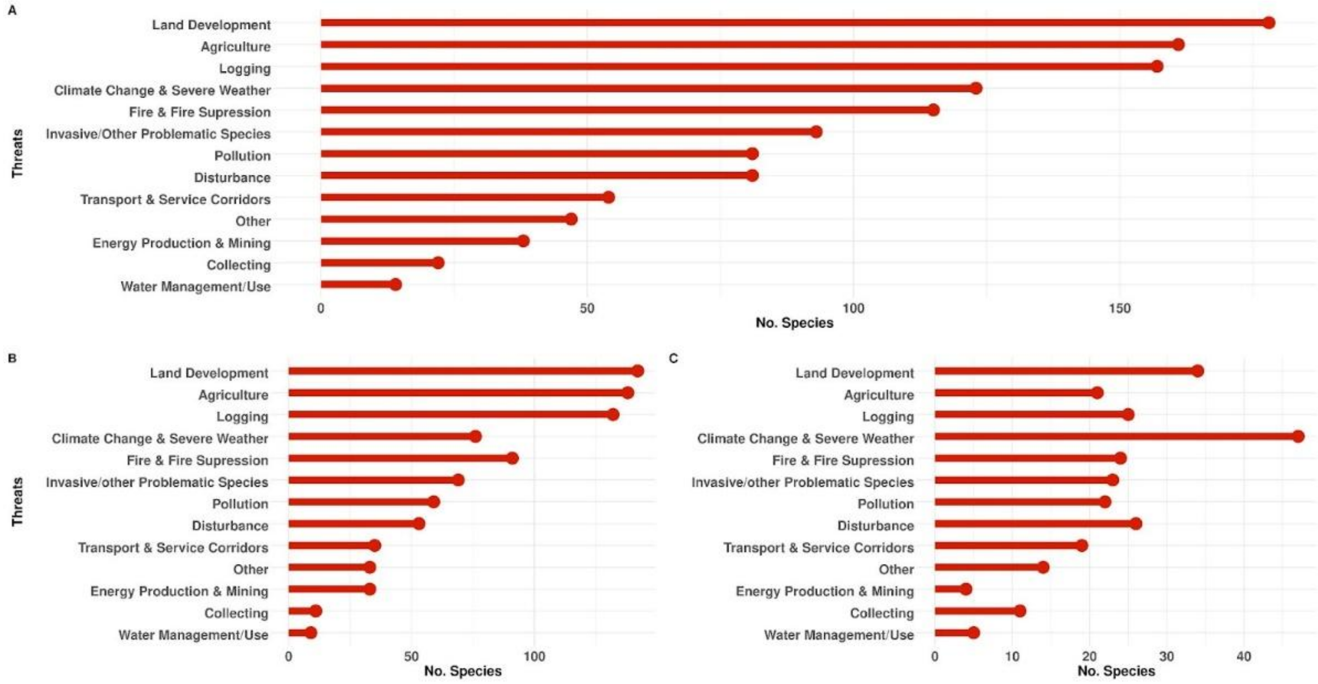


Figure 10. Threats identified for globally threatened and near-threatened: (**A**) all fungi (n = 345); (**B**) nonlichenized fungi; (**C**) lichens. This compilation was based on the qualitative listing of threats for each assessed species, and the relative size of the bars does not reflect the relative significance of each threat. NT species are included, as understanding their threats is needed to mitigate further population loss.

In regard to threats across geographic areas, considering Basidiomycota, the most frequently listed threats in Palearctic are logging (65 species), residential and commercial development (58), agriculture (44), and pollution (44) (Figure 11). For Australasia and Oceania, the top listed threats differ, being invasives/other problematic species (23 species), development (16), and fire/fire suppression (15). In the Neotropical realm, the most frequently listed threat is agriculture (68 species) followed by development (48 species) and fire/fire suppression (41 species), although logging (37 species) and climate/severe weather (36 species) are also relatively frequent. Finally, in the Nearctic, the most recorded threat is logging (26 species), followed by development (16 species) and fire/fire suppression (14 species). For lichens, the Nearctic is the only realm with a sufficient number of species assessed to break down the threat data. The most frequently listed threats to lichens in this realm are climate change/severe weather (36 species), followed by development (28 species) and logging (23 species), which is just ahead of invasives/other problematic species (22 species).

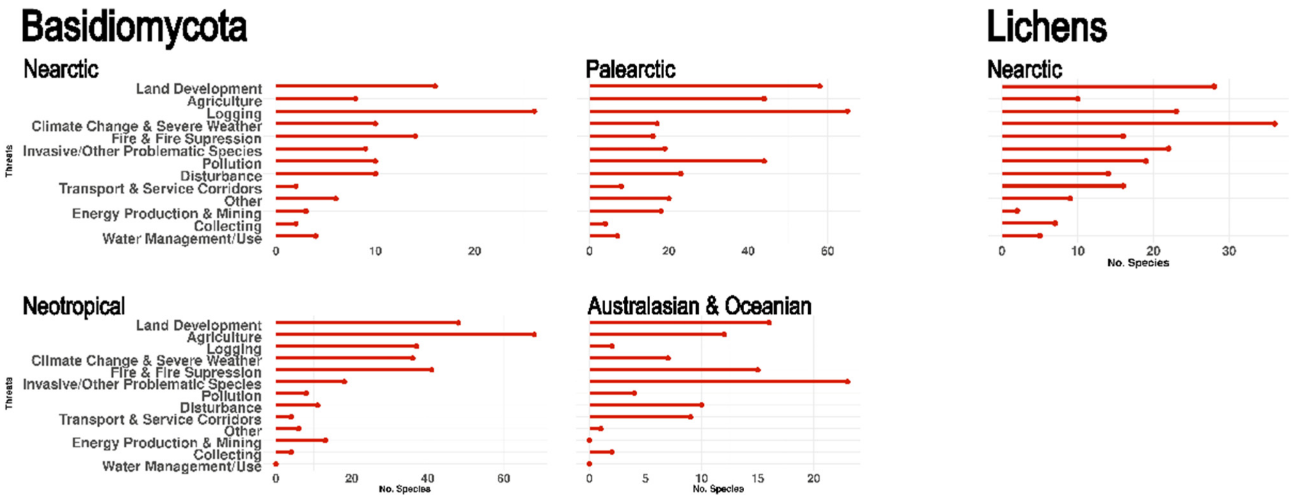


Figure 11. Threats identified for globally threatened and near-threatened Basidiomycota and lichens in the different biogeographic realms. This compilation was based on the qualitative listing of threats for each assessed species, and the relative size of the bars does not reflect the relative significance of each threat. NT species are included, as understanding their threats is needed to mitigate further population loss.

3.8. Uses

In relation to uses and trade, 173 species had at least one observed use/trade, the majority of which were for human food (133, 76.9%), mostly for species of fleshy macrofungi such as agarics, boletes, and chanterelles. Other specific uses noted for more than one species were fiber (2), medicine (9), research (4), and sport hunting/specimen collection (10, all lichens). Use is listed as a threat in only 22 of the assessed species, most commonly due to the fact of overharvesting, e.g., Butyriboletus loyo (Phillippi) Mikšík, Fomitopsis officinalis (Vill.) Bondartsev & Singer, and Ophiocordyceps sinensis (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora.

4. Discussion

The 597 fungal species currently included on the global Red List (2022-1) demonstrate that the red listing of fungi is possible across a wide range of taxonomic and functional groups from a variety of habitats across the globe. Identifying and documenting threats to fungi is critical for conservation to be initiated and carried out, either focused on fungi alone or as part of broader efforts with fungi supporting, supplementing, and adding value to the conservation of animals, plants, and habitats. The range of currently assessed fungi provides examples and templates for future assessment activities. It also highlights significant gaps in taxonomic and geographic coverage that need to be addressed to comprehensively document the threat status of fungi and to understand the relative importance of various threats.

4.1. Risk of Extinction and Criteria Used

Nearly half (48%) of globally assessed fungal species are listed under one of the threatened categories (i.e., VU, EN, and CR). When including near threatened species (NT), this number approaches 60%. In comparison, 40% of the more than 61,000 plants (including taxa commonly treated as algae) that have been globally assessed are threatened, and 168 are extinct or extinct in the wild [24]. For animals, 20% of assessed species are threatened with 816 considered extinct or extinct in the wild [24]. The much higher proportion of fungi currently assessed as threatened most likely reflects that red listing of fungi is at an early stage relative to other taxonomic groups, efforts to date have focused on species already known (from national lists) to be or suspected of being threatened, and very few fungi have been assessed. This situation also explains the relatively low proportion of fungi (<10%) listed as data deficient (DD) compared to animal groups (with the exception of birds), where the proportion of DD ranges from over 14% for Chordata to nearly 30% for invertebrates [34]. The low number of DD fungal species reflects the decision of assessors to select species with sufficient data to determine a threat category rather than an indication of our knowledge of fungal diversity and distribution. Current efforts to comprehensively sample select fungal taxa (e.g., Cantharellus and leafy Parmeliaceae) along with a potential future Sampled Red List Index will provide a more comprehensive understanding of the distribution of different threat statuses within groups of fungi. While such comprehensive assessments provide information on specific groups and enable comparisons across taxonomic groups, the focus for fungal red listing needs to continue to be on selected species potentially threatened to provide the data needed for conservation action.

The detailed elaboration of methodologies for threat listing of fungi by Dahlberg and Mueller [16] has enabled mycologists to utilize all assessment criteria, except for criterion E (i.e., quantitative analysis), which is the most rarely used criterion across all taxonomic groups [24]. In particular, the methodology for converting observations on sporing bodies (of which there may be numerous arising from the one genet) to counts of mature individuals has facilitated listing under criteria C and D, which require an estimate of the number of mature individuals. Their suggested method for estimating the time period appropriate to calculate population change for various trophic guilds and habits facilitated the use of criteria A and C1 (i.e., rate of population change).

Differences in the distribution of the four assessment criteria across the different fungal taxa (e.g., class) and trophic guilds reflect both the size and geographic distribution of the fungal species assessed and actual population trends. Criterion B (i.e., geographic range and fragmentation, decline, and/or extreme fluctuations) has relatively rarely been used for nonlichenized fungi. This may, in part, be due to the challenges of inferring the actual distribution ranges of species known from a limited area. Additionally, while the overwhelming majority of spores from a sporing body are typically deposited within a short distance, less than a few meters [35], occasional successful medium- and long-distance dispersal events contribute to the observed broader distributions. In contrast to nonlichenized fungi, more lichenized species are listed under criteria B and D (i.e., range restricted and/or very small population size) than other growth forms. Lichens are often long-lived on the substrata where they occur, which enables a more complete understanding of their distribution and population size relative to other fungal life forms. Mutualist-ectomycorrhizal fungi are predominately listed under A or C due to the fact of their often large distribution range and susceptibility to rapid population decline if their obligate plant hosts are threatened by rapid land use changes.

4.2. Threats

Not surprisingly, fungi face the same threats as animals and plants, i.e., loss and degradation of habitat, pollution, pressure from invasive species, and direct and indirect impacts of climate change (Figures 10 and 11). Most fungal species face multiple threats which act synergistically and substantially increase the local and regional extinction risk. Thus, the data extracted from the Red List do not permit quantifying the general relative impact of the different individual threats. However, the relative importance of threats for each individual species is usually included in the assessment documentation, and the accumulation of information on threats included in the assessments is one of the most important outcomes of the increased number of fungi on the Red List.

Loss and degradation of habitat is the primary listed threat to fungi. However, the drivers of these changes differ in different parts of the world [36]. A majority of the currently listed fungal species are from developed regions of Western Europe, North America, and the Atlantic Coastal Region of Brazil (Figure 9). Thus, it is not surprising to see land development (i.e., residential and commercial development, which is common in those regions [37–39]), as the most frequently listed threat for all currently listed threatened fungi as well as for all listed nonlichenized species. In other areas, logging and continued conversion to agriculture, including the planting of exotic tree plantations, are the most frequently listed cause of habitat loss. Intensified forestry has further changed and deteriorated the habitat of many fungi confined to these habitats. Climate change/severe weather can also drive habitat degradation, e.g., desertification, drying of cloud forests, and saltwater intrusion due to the fact of increased storm intensity [40]. The relative frequency and significance of threats, therefore, will likely change with an increase in assessments of fungi from additional regions and habitats.

Other human-induced disturbances and stresses are also frequently listed threats to fungi. These include direct and indirect impacts of fire, invasive species, pollution, and climate change (Figures 10 and 11). Fire, either naturally caused or set by humans, greatly impacts habitat availability and quality and can have devastating effects on fungi, especially in areas where fire regimes are more intense and larger than historical baselines [41,42] (e.g., Hypotrachyna riparia McCune [43] and Bondarzewia retipora (Cooke) M.D. Barrett [44]). For example, recent intense fires in the western United States and Australia have destroyed thousands of hectares of critical habitat for fungi associated with old-growth forests. In addition to the negative habitat impacts caused by exotic invasive species, introduced exotic fungi have been shown to compete and sometimes replace native fungi, e.g., Amanita fuligineodisca Tulloss, Ovrebo & Halling, an obligate ectomycorrhizal fungus found in Central America, is being replaced by exotic ectomycorrhizal species that have escaped from introduced pine plantations [45].

The threats listed to both nonlichenized fungi and lichens fall into two major categories: (1) atmospheric threats including climate change and air pollution; (2) land-based threats, which lead directly to habitat loss or degradation [46]. Lichens, in particular, grow as persistent and perennial thalli that readily absorb atmospheric pollutants and respond directly and sensitively to air humidity and temperature [47]. The intrinsic relationship between lichens and atmospheric conditions makes them excellent air pollution biomonitors, a utility of theirs that has been harnessed for decades [48,49]. Pollution, especially nitrogen deposition and runoff from agricultural fields, has a significant negative impact on ectomycorrhizal fungi (e.g., [50–52]). Increased nitrogen, due to the fact of atmospheric deposition and fertilization, is the major threat to and cause of decline in wax cap fungi in European seminatural grasslands [53]. Globally, species have experienced significant population declines due to the fact of air pollution in recent decades, and this threat has decreased in some parts of the globe while increasing in others [54]. Climate change, the most frequent threat recorded for the currently published set of lichen assessments, can also cause direct mortality of lichens, especially for species that are dependent on cool, humid conditions growing in areas that are becoming significantly hotter and drier [55] (e.g., Lepraria lanata Tønsberg [56], see Box 1). Indirect climate change effects, such as sea-level rise and saltwater inundation during storms, are a further threat to some species [57] (e.g., Seirophora aurantiaca (R. Br.) Frödén [58]). Climate change impacts on nonlichenized fungi include changes in phenology [59–61] and asymmetrical responses by hosts and fungal symbionts [62]. The suite of threats that lead to habitat loss and degradation affect fungi similarly to many other groups of organisms, including logging of old-growth forests and wildfires, to which mycorrhizal fungi and lichens are particularly sensitive. Many mycorrhizal fungi and lichen species are completely dependent on mature, intact forests and forest continuity, and some do not recolonize second-growth forests [63–65] (e.g., Calicium sequoiae C.B. Williams & Tibell [66], Xylopsora canopeorum Timdal, Reese Næsborg & Bendiksby [67], Phylloporus fibulatus Singer, Ovrebo & Halling [68], and Gastrolactarius camphoratus (Singer & A.H.Sm.) J.M. Vidal [69]). Thus, logging of old-growth forests leads to the irreversible loss of some mycorrhizal fungi and lichen species. Most fungi species face multiple threats, which then act synergistically and increase their extinction risk substantially.

4.3. Gaps

The data discussed in this paper are important, as they provide the first summary and analysis of the threat status of fungi as well as a summary of the threats they face at the global scale. However, it is important to note that our knowledge of the threat status of fungi remains woefully incomplete. Only 597 of the 150,000 currently described species of fungi [70] out of an estimated 2-4 million species [3] have been globally assessed. Furthermore, the selection of species assessed so far has been taxonomically and geographically biased. While these gaps are significant and need to be addressed, to a large extent, the data presented here mirror the data on threats reported in the more than 40 published national assessments and red lists [25,26].

All currently published globally assessed fungal species are macrofungal or lichenized members of Ascomycota or Basidiomycota, reflecting the fact that almost all macroscopically visible fungi belong to these two groups. While these phyla contain the vast majority of the species in the kingdom Fungi [71,72], they represent only two of the 8-12 recognized fungal phyla [73]. Diverse and ecologically important phyla, such as Chytridiomycota and Mucoromycota, are not represented. In relation to assessments, there are two issues that are prevalent among the underrepresented phyla. Firstly, almost all are microfungi and challenges persist in interpreting the key data needed for carrying out assessments for microfungi, e.g., defining and counting the number of mature individuals of a species, even more so for those that are not culturable. Secondly, some are single celled, as are many chytrid species, and therefore cannot be assessed using the IUCN criteria, which were developed for multicellular organisms. Among Ascomycota and Basidiomycota, there are also numerous microfungi and some single-celled organisms (such as yeasts). While assessing microfungi and single-celled fungi using IUCN Red List criteria is challenging or not applicable, some species with these characteristics are likely under threat, and they need attention by the conservation community [74].

Within Ascomycota and Basidiomycota there is significant taxonomic bias, with 92% of the assessed species belonging to two classes: Lecanoromycetes (lichenized ascomycetes) and Agaricomycetes (mushrooms and related species). Some taxonomically and phylogenetically diverse classes, such as Dothideomycetes, Eurotiomycetes, Pucciniomycetes, and Ustilaginomycetes, are either very sparsely included or are lacking completely. This bias in taxon selection for assessments, in part, reflects those groups for which early conservation initiatives led to regional and national red lists, which provided data and interest to support the global assessments. In addition, lichens and macrofungi, especially mushrooms (agarics), have long been popular targets of citizen science initiatives, such as mapping schemes, contributing to a larger pool of data for these taxa.

Ecological biases also are evident in the species that have been selected for assessment. Evaluated species are dominated by ectomycorrhizal species. This pattern conflicts with global trends observed for functional groups in fungi (e.g., [17]) in which, at a worldwide scale, saprotrophs tend to be dominant. This imbalance of trophic guilds is partially due to the prevalence of large, easily observed agarics in the dataset, which are often ectomycorrhizal. Additionally, many of the workshops focused on fungi from forests dominated by ectomycorrhizal host trees, and the threats to forest trees are often well known and can be used to infer threats to fungal partners.

Species currently assessed and published also reflect a significant geographic bias. Most of the listed species occur in Western Europe, North America, and specific regions of South America (northern montane forests, Coastal Atlantic Region, and Patagonia). In the Neotropics, the number of assessed species is relatively high in Argentina, Brazil, Chile, and Colombia, reflecting countries where the efforts of local mycologists have been concentrated. Coverage of species from sub-Saharan Africa and much of Southeast Asia is limited or absent. Some countries with a high potential number of endangered species, such as Indonesia and Madagascar, have no or very few fungi assessed.

It is important to note that although there are large gaps (and always will be) in the species assessed for a megadiverse kingdom such as Fungi, each assessment provides important official knowledge that identifies species needing attention along with information that documents and enables the required conservation actions. As conservation decisions are based on what is known, continued and increased efforts to assess fungal species that are potentially in need of attention is a priority.

4.4. Future Efforts

Addressing gaps in the taxonomic and geographic representation of fungal species on the Red List will require creative solutions. While current efforts have been successful in engaging the mycological community and in generating the first rigorous, significant data on the threat status and threats of fungi, they are inadequate to meet the scale of the challenge.

The rapid increase in the number of assessed species corresponds to the efforts of the GFRLI to stimulate mycologists to collate information and make assessments at the global scale. However, the species currently on the Red List largely reflect the location of mycologists with expertise and interest in fungal conservation and who are adequately resourced to be able to undertake data collection and assessments. Red List workshops have been shown to be successful in building the capacity of mycologists to undertake threat listing, especially in regions where threat listing had not been carried out systematically at the country level. Therefore, organizing workshops that focus on underrepresented regions should be a priority. A compilation of national and regional threat lists for fungi would be a useful resource to guide future activities around the globe, both as an indication of species to prioritize for assessment and as a source of information upon which to base assessments [25,26].

For regions and/or taxonomic groups where there is sufficient knowledge, future red listing activities can work through species by synthesizing existing knowledge. For example, it is possible to infer a species' potential range and assess potential threats and their intensity when the ecology of a fungal species is reasonably well known in relation to host and/or habitat specificity. Data on the distribution of fungal hosts and associated plants and animals are available through the Global Biodiversity Information Facility (GBIF). A partnership between GBIF and the IUCN Red List Unit has created the functionality to enable one to search and filter species occurrence records based on their global extinction risk [75]. However, there remain regions and taxa for which new information needs to be gathered before red listing is possible. The efficiency of assessments can be improved by sharing information on potential threats and their intensity across workshops including fungi-focused as well as geographic-focused animal and plant workshops, e.g., information on forest cover changes or mining activity transcends taxonomic groups.

Novel approaches to identifying fungi at risk include utilizing the unmet potential of cross-matching of hosts that have already been threat listed (such as trees) with fungi that have a high preference for a particular host. Similarly, there should be a focus on identifying fungi localized in highly threatened vegetation types or habitats, as these fungi are often going to be similarly threatened.

Specialist groups within the IUCN Species Survival Commission (SSC) have played a key role in facilitating assessments. There are currently five specialist fungi groups within the SSC, and these groups have organized and/or facilitated workshops and other assessment efforts (e.g., Mushroom, Bracket and Puffball, and Lichen Specialist Groups). Planned establishment of additional specialist groups focused on underrepresented taxa will facilitate increasing taxonomic coverage. In addition, coordination among fungal specialist groups is improving through efforts by coordinators and staff at the IUCN SSC affiliated Global Center for Species Survival at the Indianapolis Zoo.

For geography, the gaps revealed will assist in the placement of future training sessions and assessment workshops. National Fungal Conservation Specialist Groups are also being developed within the SSC to build capacity, further assessment efforts, initiate conservation actions, and engage with regional conservation plans and policy efforts.

Focusing on comprehensive global assessments of specific taxa, such as is occurring with Cantharellus and as is planned for the leafy Parmeliaceae, will provide a better understanding of the threat status within groups of fungi. While a Sampled Red List approach [76–78] has been used to obtain a comprehensive picture of how extinction risk categories and threats are distributed among the full spectrum of certain large animal and plant groups, such an approach for fungi would prove minimally useful due to the great number of species that would be assessed as Data Deficient (DD) given the current and near term state of knowledge of fungal diversity and distribution, e.g., David Minter's semi-automated sampled fungal red list [79].

Because fungal diversity and distributions are still poorly documented, there is great opportunity for discovery. This provides opportunities for engaging amateur mycologists and other community scientists. Indeed, involving citizen scientists is our best hope for documenting at scale what species are occurring where and when, and how these patterns are changing. The information posted on platforms such as iNaturalist (https://www.inaturalist.org/) is greatly increasing our knowledge of the distribution of macrofungi, lichens, and even some microfungi—there were 6.5 million fungal observations posted to iNaturalist by 525,000 observers at the time of this writing. Of course, the quality of observations and amount of metadata varies greatly, and only high-quality observations can be used for documenting the diversity, distributions, and plant and habitat associations. To address this, organizations such as the Fungal Diversity Survey (FunDiS) in the US have developed curated databases of vetted iNaturalist postings (https://Fundis.org). More targeted engagements with citizen scientists have proven highly valuable [80]. Projects such as Australia's Fungi-map (https://fungimap.org.au/), UK's Lost and Found Fungi Project (https://www.kew.org/read-and-watch/lost-and-found-fungi), and the US' Rare Fungi Challenges (https://fundis.org/protect/take-action) have generated rigorous data used in assessments and conservation planning.

An important emerging tool for refining species distributions and rarity is to mine the massive and fast-growing libraries of environmental DNA from metabarcoding activities [81–84]. At least in the near term, these data may primarily be useful for moving NT or DD species to LC by demonstrating commonness across wide distributions (remembering that widespread species may still be threatened due to the fact of population declines caused by factors such as habitat loss and degradation). In contrast, for rare species, the sampling in eDNA libraries will rarely be dense enough for any significant representation, and the sampling intensity required to regularly pick up rare species is not feasible at large scales. The most promising use of eDNA in fungal conservation is as a complement to the monitoring of sporing bodies of rare species at the population level, where metabarcoding has potential for detecting mycelia of rare species to counter the difficulties of the often ephemeral and sporadic production of sporing bodies. DNA fingerprinting can also provide significant information for establishing a population's genetic structure to inform management.

Efforts are ongoing to develop automated methods to identify species of Least Concern (LC) so that assessors can focus on species in need of conservation. Such computer-based tools have been developed for plants [85]. However, this tool primarily uses distribution data and calls out species with ranges too large to assess under the B criterion. This works for plants, as many threatened plant species are range restricted. As documented in Figure 4, species of fungi have rarely been listed using only the B criterion, as most fungi are not range restricted [86]. Current efforts are investigating ways to also incorporate available land-use change data into the evaluation. If successful, this will enable the completion of over 20,000 assessments over the next 10 years. An additional challenge with utilizing automated methods is that most fungal species are represented in databases by few collections and/or observations. Consequently, while there is hope that automation will be successful in identifying some LC species, efforts to document threatened fungal species is likely to continue to be driven mainly by specialists with knowledge of the population characteristics and threats of each species being assessed.

4.5. From Red Listing to on-the-Ground Actions

Threat listing has been a vital part of raising the profile of fungi as organisms that are at risk of extinction, similar to animals and plants. While the Red List does not automatically trigger on-the-ground action, the inclusion of species on the Red List, as a result of an objective and repeatable process, provides information that can be used for conservation action such as the amelioration of threats. Indeed, the process of evidence gathering that contributes to Red List assessments is an important part of the conservation cycle, with field work often motivated by the identification of gaps in the knowledge and using data in the assessment for developing and implementing conservation actions (e.g., [87,88]).

It should be stressed that red listing is a first step, which alone may not have any practical effect on the extinction risk without subsequent action. Therefore, it is vital to follow up with the creation and implementation of action plans and practical measures such as inclusion of known sites of threatened species in protected areas. An example of significant legislative consequences of global listing comes from the United Kingdom, where globally threatened fungi were recently added as a criterion in official guidelines for the selection of sites to be considered for legal protection [89,90]. According to these guidelines, all sites with viable populations (lichens) or persistent fruiting populations (nonlichenized taxa) of fungi globally assessed as CR should be considered for legal protection. Furthermore, similar protection should be extended to a subset of national sites for species with global assessments of EN and VU. Around the world, it will be necessary to follow up on those fungal species already globally red listed to ensure that where there is legislative protection at national levels, species are formally proposed for inclusion under relevant national lists.

Published assessments of the Red List are a source not only of the threat categorization but also for information on distribution, habitat, ecology, use and trade, threats, and needed conservation actions. Thus, global Red List assessments of fungi can be referenced and used by local land managers. They are especially useful where fungi are not included or are sparse in national and subnational conservation frameworks. In these situations, the global Red List is one of the only sources of conservation status information available for land managers and conservation practitioners interested in incorporating fungi in conservation planning and action. An example of the assessments being used is in Shenandoah National Park, Virginia, USA, where the assessment for Lepra andersoniae (Lendemer) Lendemer & R.C. Harris was integral for guiding permitted activities taking place on sensitive talus slopes throughout the park [69].

Monitoring the effectiveness of action plans is also vital. As the number of assessed fungi increases, it will be useful to revisit at least a sample of assessed species at intervals (such as decades), as suggested by the Red List guidelines [91], to check on changes to threat status and what is responsible for such changes (negative or positive). However, this has proven difficult to achieve, with re-assessments comprehensively conducted only for birds, mammals, amphibians, reef-building corals, and cycads [78]. Even groups assessed based on the Sampled Red List Index approach struggle to produce re-assessments for all relevant species [78,92]. A strategy is needed to undertake re-assessments at regular intervals in parallel with the publication of new assessments. Red listing is also a useful tool to raise awareness among the public and to make sure that local communities and organizations, such as landowners, land managers, and conservation groups, are aware of any threatened fungi that occur in their neighborhoods, as they are often best placed to carry out the on-the-ground actions required to ameliorate threats, etc.

As we gain knowledge on the ecology of individually listed threatened fungi, land management can be optimized for threatened fungi across the landscape (not just in conservation reserves) with flow-on effects for the large number of fungi for which the conservation status is unknown. Indeed, the relatively few fungi that are formally assessed carry the flag for the host, substrata, rate of population change and habitat modification, and habitat requirements of the vast numbers of as yet unassessed fungi.

5. Conclusions

Reaching the milestone of more than 500 assessed fungi prompts consideration of how the research agenda for conservation mycology can be further developed to assist both the assessment process and the implementation of management [93]. A number of themes have already been identified that remain vital, especially: (1) "How do life history characteristics (population size, turnover, size of individuals, etc.) vary across fungal morphogroups, lineages, and guilds and how to measure these?" and (2) "Are there effective surrogates for fungi in monitoring and reserve design (either other fungi or other biota)?". Practical topics in conservation biology that are well explored and implemented for many threatened animals and plants, such as translocation and ex situ conservation, need to be elaborated for conservation mycology. The recent development of "principles for conservation translocations of threatened wood-inhabiting fungi" [94] show the way forward.

Despite the gaps in our knowledge of fungal diversity, distribution, and biology, it is clear that fungi play essential roles in ecosystems. The information compiled and analyzed from the current global fungal assessments discussed in this paper identifies the key suite of threats impacting fungi. Lack of data is not a reason to delay implementing the urgent action and targeted policies needed to prevent these species from becoming extinct and the ecological consequences that would result.

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