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REVIEW**Extinction risk and threats to plants and fungi**

Eimear Nic Lughadha¹  | Steven P. Bachman¹  | Tarciso C. C. Leão¹ | Félix Forest² | John M. Halley³ | Justin Moat⁴  | Carmen Acedo⁵  | Karen L. Bacon⁶  | Ryan F. A. Brewer¹  | Gildas Gâteblé⁷  | Susana C. Gonçalves⁸  | Rafaël Govaerts⁴ | Peter M. Hollingsworth⁹ | Irmgard Krisai-Greilhuber¹⁰ | Elton J. de Lirio¹¹ | Paloma G. P. Moore¹  | Raquel Negrão¹  | Jean Michel Onana¹² | Landy R. Rajaovelona^{1,13} | Henintsoa Razanajatovo^{1,13} | Peter B. Reich^{14,15} | Sophie L. Richards¹  | Malin C. Rivers¹⁶ | Amanda Cooper^{4,17} | João Iganci^{18,19} | Gwilym P. Lewis²⁰ | Eric C. Smidt²¹ | Alexandre Antonelli^{22,23}  | Gregory M. Mueller²⁴ | Barnaby E. Walker¹

¹Conservation Science Department, Royal Botanic Gardens, Kew, Richmond, UK

²Analytical Methods, Royal Botanic Gardens, Kew, Richmond, UK

³Laboratory of Ecology, Department of Biological Applications & Technology, University of Ioannina, Ioannina, Greece

⁴Bioinformatics and Spatial Analysis Department, Royal Botanic Gardens, Kew, Richmond, UK

⁵Department of Biodiversity and Environment Management, Faculty of Biological and Environmental Sciences, Campus of Vegazana, University of León, León, Spain

⁶Botany & Plant Sciences, School of Natural Sciences, National University of Ireland, Galway, Ireland

⁷Equipe ARBOREAL, Institut Agronomique néo-Calédonien, Mont-Dore, New Caledonia

⁸Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

⁹Royal Botanic Garden Edinburgh, Edinburgh, UK

¹⁰Mycology Research Group, Division of Systematic and Evolutionary Biology, Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria

¹¹Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

¹²Systematics, Biodiversity and Conservation of Plants, Faculty of Science, University of Yaoundé I & National Herbarium of Cameroon, Yaoundé, Cameroon

¹³Kew Madagascar Conservation Centre, Antananarivo, Madagascar

¹⁴Department of Forest Resources, University of Minnesota, St. Paul, MN, USA

¹⁵Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia

¹⁶Botanic Gardens Conservation International, Surrey, UK

¹⁷Department of Biological Sciences, Royal Holloway, University of London, Egham, UK

¹⁸Instituto de Biologia, Departamento de Botânica, Universidade Federal de Pelotas, Pelotas, Brazil

¹⁹Instituto de Biociências, Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

²⁰Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond, UK

²¹Departamento de Botânica, Universidade Federal do Paraná, Curitiba, Brazil

²²Royal Botanic Gardens, Kew, Richmond, UK

²³Gothenburg Global Biodiversity Centre, Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

²⁴Negaunee Institute for Plant Conservation Science and Action, Chicago Botanic Garden, Chicago, IL, USA

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Correspondence

Eimear Nic Lughadha, Conservation Science
Department, Royal Botanic Gardens, Kew,
Richmond, UK.
Email: e.niclughadha@kew.org

Societal Impact Statement

There is increasing awareness that plants and fungi, as natural solutions, can play an important role in tackling ongoing global environmental challenges. We illustrate how understanding current and projected threats to plants and fungi is necessary to manage and mitigate risks, while building awareness of gaps and bias in current assessment coverage is essential to adequately prioritize conservation efforts. We highlight the state of the art in conservation science and point to current methods of assessment and future studies needed to mitigate species extinction.

Summary

Plant and fungal biodiversity underpin life on earth and merit careful stewardship in an increasingly uncertain environment. However, gaps and biases in documented extinction risks to plant and fungal species impede effective management. Formal extinction risk assessments help avoid extinctions, through engagement, financial, or legal mechanisms, but most plant and fungal species lack assessments. Available global assessments cover c. 30% of plant species (ThreatSearch). Red List coverage overrepresents woody perennials and useful plants, but underrepresents single-country endemics. Fungal assessments overrepresent well-known species and are too few to infer global status or trends. Proportions of assessed vascular plant species considered threatened vary between global assessment datasets: 37% (ThreatSearch), and 44% (International Union for Conservation of Nature Red List of Threatened Species). Our predictions, correcting for several quantifiable biases, suggest that 39% of all vascular plant species are threatened with extinction. However, other biases remain unquantified, and may affect our estimate. Preliminary trend data show plants moving toward extinction. Quantitative estimates based on plant extinction risk assessments may understate likely biodiversity loss: they do not fully capture the impacts of climate change, slow-acting threats, or clustering of extinction risk, which could amplify loss of evolutionary potential. The importance of extinction risk estimation to support existing and emerging conservation initiatives is likely to grow as threats to biodiversity intensify. This necessitates urgent and strategic expansion of efforts toward comprehensive and ongoing assessment of plant and fungal extinction risk.

KEYWORDS

automated conservation assessments, biodiversity loss, extinction debt, extinction risk, Global Strategy for Plant Conservation (GSPC) Target 2, International Union for Conservation of Nature (IUCN) Red List of Threatened Species, phylogenetic diversity (PD)

1 | INTRODUCTION

Reports of species extinctions can cross the boundary of scientific and public interest. Accumulation of scientific evidence of both extinctions and extinction risk and growing public awareness, through movements like “Extinction Rebellion”, confirms this as an area of global concern. However, animal extinctions attract considerably more attention and research than plants or fungi. While global status and trends in extinction risk for major vertebrate groups have been documented over decades, most plant and fungal species lack a global extinction risk assessment (BGCI, 2020; IUCN, 2020a). Lack

of knowledge of which plants and fungi are most at risk, of what threatens them, and of how this is changing over time limits our ability to inform conservation policy and action, to protect species and areas most at risk, and ultimately to support plant- and fungal-based solutions to the critical challenges facing humanity.

Scientists have devoted much time and effort to research concerning the global status of plant and fungal species (Juffe-Bignoli et al., 2016), with considerable success. Numbers and proportions of species assessed for their extinction risk have increased rapidly in recent years, albeit from very low baselines (Bachman et al., 2019). However, these many independent or loosely coordinated efforts

have resulted in a body of knowledge of extinction risk for plants and fungi that is still far from globally representative.

Gaps and biases in our understanding of extinction risk in plants and fungi result not only from the well-documented geographic, taxonomic, and temporal gaps and biases in baseline biodiversity information (Meyer, Weigelt, & Kreft, 2016; Paton, 2020) on which extinction risk assessments are based. They also arise, directly and indirectly, from the diversity of motivations driving selection of species for assessment, resulting in prioritization for assessment of, for example, species of actual or potential use to humans (e.g., Davis et al., 2019), species occurring or confined within defined political boundaries (e.g., Martins, Martinelli, & Loyola, 2018; Onana, Cheek, & Pollard, 2011; Raimondo, von Staden, & Donaldson, 2013), and species or groups considered a priori to have relatively high extinction risk (Goettsch et al., 2015). The combined effect of such diverse priorities over two decades has produced a body of evidence in which gaps and biases confound attempts to characterize global extinction risk for major groups.

The aim of this review is to quantify coverage, gaps, and biases in knowledge of extinctions and extinction risk of known plant and fungal species, and to explore how limitations in our protocols and lacunae in our understanding of pattern or process may affect current estimates of extinction risk. We also consider emerging trends in extinction risk, with new data for megadiverse Brazil and Madagascar, and an overview of some new metrics and technologies with potential to transform this field in the coming decade.

Although plant and fungal diversity include the taxonomic, (phylo) genetic, and functional diversity within species, between species, and of the ecosystems of which they form part, we focus our quantitative overview primarily on taxonomic diversity at the species level because species represent the most fundamental unit of biodiversity, in biology and conservation science. Species represent the taxonomic level at which plant and fungal diversity is most consistently recorded and analyzed for the purposes of inventory, monitoring, or monography as well as for conservation assessment, analysis, action, and legislation. We analyze available species extinction risk assessments, accounting for known biases wherever possible, and apply a novel approach to predicting extinction risk of unassessed species to refine estimates of proportions of plants threatened globally (Section 2).

Phylogenetic and functional diversity capture additional facets of diversity that are available for relatively small proportions of plants and fungi and thus not yet highly informative in a global review (Brummitt, Araújo, & Harris, 2020; Vellend et al., 2017). Understanding of phylogenetic diversity (PD) is particularly important in a conservation context as it predicts both known and unknown attributes of species and lineages (Corlett, 2020; Owen, Gumbs, Gray, & Faith, 2019). We provide a qualitative overview of PD and also of extinction debt and key threat drivers which are not or imperfectly captured in species extinction risk assessments (Section 3).

We highlight the value of extinction risk assessments as a conservation tool, despite their many limitations (Section 4). We present new trend data for extinction risk in plants (Section 5), and review approaches and resources for accelerating production of extinction risk assessments (Section 6) for plants and fungi.

The importance of extinction risk estimation to support existing and emerging conservation initiatives is likely to grow as threats to biodiversity intensify. We call for urgent and strategic expansion of efforts toward comprehensive and ongoing assessment of plant and fungal extinction risk. Artificial intelligence can help prioritize assessment resources while the latest spatial and genomic data and techniques can be harnessed to achieve robust and rapid assessments, thus closing gaps and known bias in plants and fungal extinction risk knowledge.

2 | GLOBAL STATUS OF PLANTS AND FUNGI AS EVIDENCED BY EXTINCTION RISK ASSESSMENTS

2.1 | Red List coverage of plants and fungi

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2020a, hereafter Red List) is the most comprehensive and authoritative source on global extinction risk for species. Nonetheless, just 116,177 of the conservatively estimated 2.1 million known species of eukaryotes are represented by global Red List assessments, equivalent to c. 5.5% coverage (IUCN, 2020a). Coverage of fungi is much lower; only 285 of 148,000 (Species Fungorum, 2020) described fungal species (0.2%) are assessed on the Red List. Plant coverage doubled recently, reaching 10% (IUCN, 2020a), including over 19,000 assessments added in 2017–2019. However, this percentage hides some extremes: cryptogams have very low coverage (mosses 1.3% and green algae <1%), insufficient to discern global threat levels. Vascular plant coverage is greater at 10.5% assessed, and of those species for which threat status could be determined, 43.7% are considered threatened (i.e., categorized as Vulnerable, Endangered (EN), or Critically Endangered (CR); see Methods S1 for upper and lower bounds for proportions threatened). Among vascular plants, most gymnosperms have been assessed, with 40% considered threatened. The larger groups of vascular plants have lower assessment coverage than gymnosperms: c. 6% for ferns and fern allies, and 10.4% for flowering plants. For these groups, c. 44% and 46%, respectively, of assessed species for which sufficient data are available are categorized as threatened. These percentages do not represent reliable global estimates for all plants due to biases in the sample assessed (2.3).

2.2 | Progress toward Target 2 of the global strategy for plant conservation

The rapid growth in plant coverage on the Red List over recent years is due in part to the Global Strategy for Plant Conservation, through which parties to the Convention on Biological Diversity (CBD) called for “assessment of the conservation status of all known plant species” by 2020 (CBD, 2012; Paton & Nic Lughadha, 2011). Responses to this target at national and international level generated global

assessments for many thousands of plant species (including assessments of single-country endemics). These were published in diverse formats (e.g., National Red Lists, online resources, and academic journals), and over 60% of the species they cover lack an assessment on the global Red List (Methods S1).

The ThreatSearch database collates digitally available, evidence-based plant assessments, and is regularly updated by Botanic Gardens Conservation International (BGCI, 2020). Bachman, Nic Lughadha, and Rivers (2018) used a snapshot of ThreatSearch (November 2016) to quantify progress toward the Global Strategy for Plant Conservation (GSPC) Target 2, after reconciling scientific names to The Plant List (TPL1.1) and assessment status to defined standards. Counting assessments matched to accepted names, 73,081 species had been assessed at global scale, representing c. 21% of known plant species. At least 27,148 species had been assessed as threatened, representing c. 8% of plant species and 30% of assessments in ThreatSearch.

We repeated the above analysis using ThreatSearch datasets from November 2016 to January 2020 (Methods S1). Our methods differed only in reconciling names, including basionyms, to the World Checklist of Vascular Plants (WCVP, 2020). Results suggest that Bachman et al. underestimated both numbers of global assessments and species assessed as threatened, probably due to the many unresolved names in TPL now resolved in WCVP. Our new analysis (Figure 1), with the new (higher) 2016 baseline, shows marked growth in total assessments (+37.2%), in global assessments matched to accepted names (+23.1%), which now equate to 28.3% of vascular plant species, and in global threatened assessments matched to accepted names (+16.1%). The proportion of assessments reporting globally threatened species decreased slightly from 36% to 34%. Of the species with a global assessment listed in ThreatSearch, 37% were assessed as threatened. Caveats concerning bias apply as for Red List (see 2.3). Nevertheless, the uplift in available global assessments is clear and encouraging.

2.3 | Biases and gaps in plant and fungal coverage on the Red List

The non-random sample of plants and fungi on the Red List results from selecting species for assessment influenced by data availability; human interest in useful, attractive, or unusual species; national assessment initiatives; and expectations that certain species or groups are exceptionally threatened (Bachman et al., 2019). These differing priorities have left biases and gaps in current assessment coverage.

We used comprehensive data from the WCVP (2020) to quantify biases in Red List coverage of vascular plants, using only assessments published since 2001 to maximize consistency (Methods S2). We considered attributes likely to have influenced assessment priorities: the life-form of the species, the family to which it belongs, on what continent the species occurs, whether the species is endemic to a single botanical country, and if the species had a recorded human use (Diazgranados et al., 2020). Definitions of continent and botanical country followed, respectively, levels 1 and 3 of the World Geographical Scheme for Recording Plant Distributions (WGSRPD; Brummitt, 2001).

We identified multiple biases and gaps in assessment coverage. Given the many national assessment initiatives responding to GSPC Target 2 (e.g., Martins et al., 2018; Onana et al., 2011; Raimondo et al., 2013) and the known propensity to assess species suspected to be threatened (Bachman et al., 2019), we expected single-country endemics to be overrepresented on the Red List. Surprisingly, species endemic to a single botanical country are slightly underrepresented on the Red List, comprising 56.0% of known vascular plants, but only 49.1% of Red List vascular plant assessments ($p < .001$, tested by binomial test). Because WGSRPD splits some large countries into smaller botanical countries, potentially reducing the numbers of species considered endemic, we repeated our analysis after reconstructing countries (following Gallagher et al., 2020), but endemic species remained underrepresented (Methods S2).

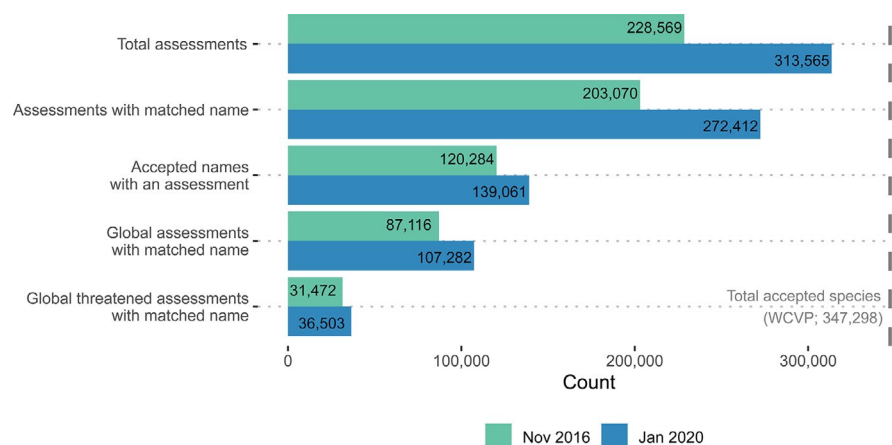


FIGURE 1 Comparison of the total number of assessments and coverage of accepted names by assessments in the ThreatSearch database for the dataset from the end of 2016 and the start of 2020. The total number of assessments includes multiple assessments at different scales for many species. After matching assessments to an accepted name, we count at most one assessment per threat level for each accepted name. Assessments were matched to species names in the World Checklist of Vascular Plants (WCVP, 2020) database

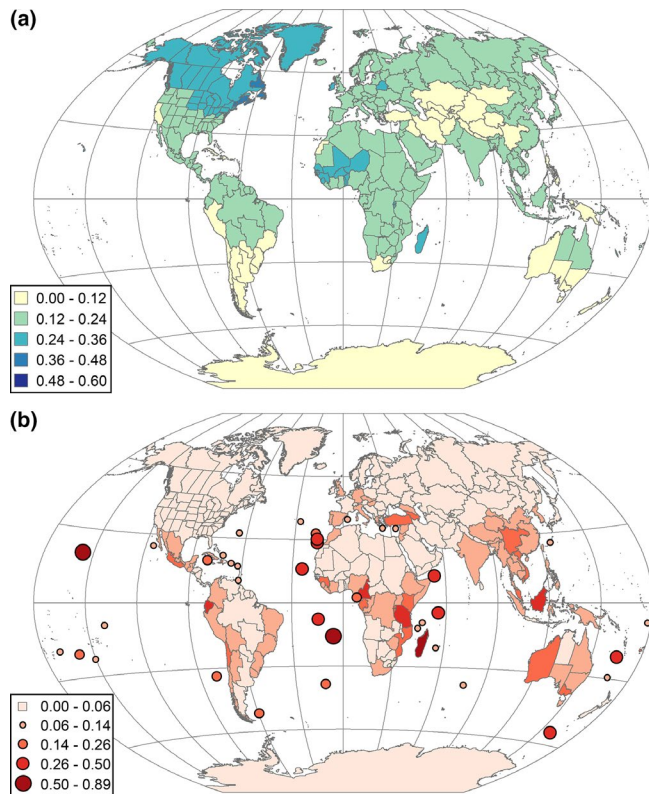


FIGURE 2 Each botanical country (WGSRPD level 3; Brummitt, 2001) colored by (a) the proportion of plant species covered by a global assessment on the Red List and (b) the proportion of assessed plant species classified as threatened. While some areas present low coverage of assessments, they stand out as presenting a relatively high proportion of threatened species, such as southern South America, South Africa, India, and southern Australia, and should be considered as high interest for future studies

Geographical biases in assessments were evident, with particular effort focused on African plants (Figure 2a), and a big gap in assessments for plants from both temperate and tropical Asia. Woody perennials were vastly overrepresented by assessments on the Red List, a bias likely to increase with the rapid progress of the Global Tree Assessment (Newton et al., 2015; Rivers, 2017). Species having recorded human use were also overrepresented, their societal importance having prompted assessment (e.g., Davis et al., 2019; Howes et al., 2020).

The impacts of targeted assessment programs on the taxonomic coverage of the Red List were evident. The most overrepresented families include those targeted by the assessment programs, such as Cactaceae (Goetsch et al., 2015) and Myrtaceae (Nic Lughadha et al., 2019). The most underrepresented families include some of the most species-rich, including Asteraceae, Orchidaceae, Poaceae, and Lamiaceae (which together comprise almost 25% of all vascular plants; Dataset S1).

Of the 285 fungi assessed for the global Red List, 234 are species of Basidiomycota, one of seven phyla of Kingdom Fungi (Mueller, Dahlberg, Scott, & Westrip, 2020). Global fungal assessments are still at early stages, so efforts focus on better known species and regions, for example agarics and Western Europe, or on

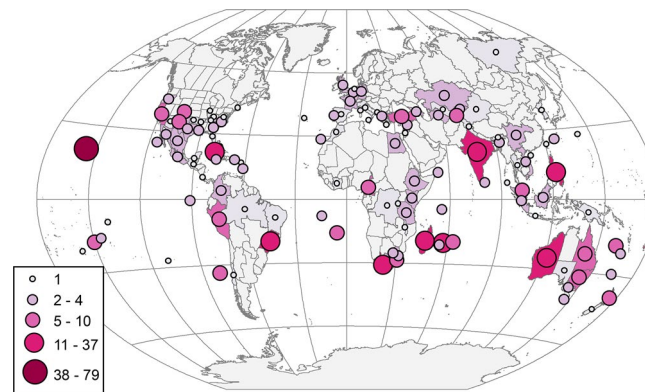
discrete habitats such as European semi-natural grasslands (Mueller, Dahlberg, & Krikorev, 2014).

Biases in species assessed on the Red List demonstrate the efficacy of targeted assessment initiatives. However, the limited coverage of fungi, of some of the largest plant families, and of Asian plants, show how far the Red List is from representing threats to global plant and fungal diversity.

2.4 | Most and least threatened plant groups

Addressing assessment coverage gaps is paramount for a realistic picture of extinction risk to plants. Varying threat levels reported for the groups of species assessed interact with these gaps and biases to distort our current picture. We applied a statistical modeling method, used successfully in recent years for predicting the outcomes of political elections from unrepresentative polls (Wang, Rothschild, Goel, & Gelman, 2015), to estimate the different levels of threat for groups defined by the attributes identified above. We trained our model on vascular plant species assessed for the Red List since 2001 for which we had both geographic and life-form data from WCVP (28,479 of 33,029 assessed species). We then applied our model to all known vascular plant species to infer their extinction risk while accounting for quantifiable biases and gaps in assessment coverage (Methods S3). Importantly, we could not quantify or factor out the bias resulting from assessors' propensity to assess species suspected to be threatened, as their motivation for assessment is not consistently recorded. Parameter estimates from our model revealed a clear, if unsurprising, increase in the odds of being threatened for species endemic to a single botanical country (Table S7). Conversely, having a recorded use reduced the odds that a species is threatened by more than half (Table S7). Contrary to our expectations, life-forms did not significantly change the odds (but see Box 1; Table S8). In geographic terms, being from Africa doubled the odds that a species is threatened, while being from Australasia roughly quartered the odds (Table S9). Taxonomic family influenced the estimated threat status: species belonging to one of 37 families in our analysis had increased odds of being threatened. These included families already recognized as having high threat levels, such as the Zamiaceae (cycads), as well as some larger families, for example Myrtaceae and Orchidaceae (Methods S3, Table S10, Dataset S2).

Predicted levels of threat for all known vascular plants from our model reveal where the Red List may currently over- or underestimate extinction risk. Comparison of predictions and Red List assessment suggests that sample bias has caused levels of threat to be underestimated in Southern America, Northern America, and tropical Asia. Myrtaceae, Lauraceae, Fagaceae, and Cyperaceae are among the families with the most underestimated level of threat (Table S11), while Arecaceae (palms) and Ebenaceae (ebony and relatives) are among those families most overestimated (Table S12). At 39.4%, the overall predicted proportion of threatened species resulting from our model is slightly lower than the proportion of vascular plants assessed for the Red List that are considered threatened: midpoint estimate 43.7% (range = 40.7%–47.5%, see Methods S1 for details).

BOX 1 Comparison of patterns in extinction risk estimates versus documented modern extinctions

Number of recorded modern extinctions in each botanical country (WGSRPD level 3) as per Humphreys et al. (2019)

Nearly 600 seed plant species have gone extinct since the time of Linnaeus (correcting for rediscovery and reclassification; Humphreys, Govaerts, Ficinski, Nic Lughadha, & Vorontsova, 2019). Although requiring regular updates, because of ongoing reports of extinction and rediscovery (Humphreys, Vorontsova, Govaerts, & Nic Lughadha, 2020), this estimate suffices to show that plant extinctions are much more numerous than those reported on the Red List, and that the ongoing rate of plant extinctions is up to 500 times the pre-Anthropocene background extinction rate for plants (De Vos, Joppa, Gittleman, Stephens, & Pimm, 2015), but lower than suggested by earlier studies. These relatively low rates are likely underestimates due to underreporting (despite the rediscovery rate) and long extinction lag times (see 3.2).

Our further analysis of the plant extinction database (Humphreys et al., 2019; Methods S6) showed that of the 10 areas with most disproportionately high numbers of recorded extinctions, nine are islands (the exception being India). Hawai'i and St. Helena have the largest proportion of their flora recorded as extinct (7.3%). Elevated extinction levels on islands mirror higher levels of species assessed as threatened for the Red List. Many of the islands most overrepresented in extinctions are also overrepresented in threatened species, with Hawai'i and St. Helena again most overrepresented (Figure 2b). In contrast, megadiverse Madagascar and Ecuador are overrepresented in threatened species but not recorded extinctions. This may suggest that extinction is more likely on islands, or that assessors can be more confident concerning extinction of species endemic to islands, both being consistent with the finding that reported plant extinctions from islands are less likely to be refuted by subsequent rediscovery (Humphreys et al., 2019).

Similarly, Humphreys et al. (2019) reported extinctions to be concentrated in woody perennial plants, but suggested that this might result from relatively high interest in trees, rather than an elevated risk of extinction. This suggestion is consistent with our findings (2.3, 2.4) that woody perennials are overrepresented on the Red List but not at greater risk of extinction, after correction for known bias.

Strikingly, all of the above estimates greatly exceed the estimate of 21% threatened that was derived from the random samples of plant diversity used in the Red List Index for Plants (Brummitt, Bachman, Aletrari, et al., 2015). More detailed analysis of the factors underlying this difference in estimates is beyond the scope of this study. However, the propensity of assessors to assess species and groups suspected to be threatened probably explains some of the difference, causing the Red List to overestimate extinction risk for incompletely assessed groups, an effect which we could not quantify for inclusion in our model. The random samples assessed for the Red List Index for Plants were designed specifically to avoid such selectivity on the part of assessors (Brummitt, Bachman, Aletrari, et al., 2015). Conversely, the assessment approach applied for the first phase of the Red List Index for Plants may have underestimated extinction risk, with 59% of assessments being based on geographic range (Red List criterion B; Brummitt, Bachman,

Griffiths-Lee, et al., 2015). The past decade has seen increased use of population size reduction estimates or inferences (criterion A), which are more likely to result in plant species being assessed as threatened (Rivers, Brummitt, Nic Lughadha, & Meagher, 2014).

Both the parameter estimates and predicted proportions of threatened species from our model identify potential future assessment priorities. Single-country endemics, currently underrepresented on the Red List but with increased odds of being threatened, may be considered priorities for assessment depending on the national context. Other priorities should include large families pinpointed in our gap analysis as underrepresented on the Red List. These encompass some of the most threatened families and also families where threat has been most underestimated. Improved coverage for Asia (underrepresented on the Red List and underestimated level of threat for tropical species) could be achieved by renewed efforts to incorporate national assessments of endemic species (e.g., Qin et al., 2017).

3 | BEYOND EXTINCTION RISK ASSESSMENTS

Extinction risk assessments represent vital contributions to understanding the status of and threats to plant and fungal species, and to a global overview of biodiversity. However, there are important aspects of diversity loss which these assessments capture only incompletely or indirectly, if at all. We consider loss of evolutionary potential, species loss due to slow-acting threats, and the major drivers threatening species.

3.1 | Phylogenetic signal in extinction risk and EDGE

Extinction results not only in species loss, but also in loss of the unique evolutionary history that these species represent, including suites of irreplaceable features and unique combinations of functions (Pimiento, 2018). An isolated species on the tree of life (sole survivor of an old lineage) represent more unique evolutionary history than a recently evolved species with several close relatives. Importantly for long-term conservation, but difficult to quantify, species extinction also reduces overall evolutionary potential, or the ability of a group of organisms to survive and adapt to future environmental changes.

Most organisms have several close relatives and thus contribute relatively little to the overall evolutionary history of their group. Deeper branches of the tree of life go extinct only when all the species they subtend vanish, an improbable scenario if extinction occurs randomly (Purvis, Agapow, Gittleman, & Mace, 2000). Simulations show that large numbers of random extinctions could have little effect on overall amounts of evolutionary history (Nee & May, 1997). However, increasing molecular and palaeontological evidence indicate that extinction is not random, but clustered in certain lineages (Davies, 2019; Davies et al., 2011; Leão, Fonseca, Peres, & Tabarelli, 2014; Tanentzap, Igea, Johnston, & Larcombe, 2020; Vamosi & Wilson, 2008) and linked to lineage age (Hagen, Andermann, Quental, Antonelli, & Silvestro, 2017), although not all studies find phylogenetic clustering in plant extinction risk (Cardillo & Skeels, 2016). In Africa's Eastern Arc Mountains, phylogenetic signal of extinction risk varies between Red List threatened categories, with no significant clustering for EN or CR plant species, while Vulnerable species are clustered (Yessoufou, Daru, & Davies, 2012). Furthermore, documented plant extinctions show no phylogenetic signal (Humphreys et al., 2019; Box 1). Further research is needed on the extent to which extinction risks tend to affect related plant species and the likely consequences of such clustering. Some studies indicate that even significant clustering of extinction risk does not necessarily equate to heavy loss of evolutionary history (Parhar & Mooers, 2011; Thuiller et al., 2011), while others show the opposite (Daru, Yessoufou, Mankga, & Davies, 2013; Eiserhardt, Borchsenius, Plum, Ordonez, & Svenning, 2015).

Despite uncertainties, there is growing focus on approaches to factor phylogeny into conservation prioritization (Pellens & Grandcolas, 2016). Prominent among these is PD (Faith, 1992), offering benefits including its potential use as proxy for feature diversity, that is the diversity of attributes or traits of species, and its ability to maximize retention of the evolutionary potential of species and their

future unanticipated possible benefits for human society and nature (Forest et al., 2007; Larsen, Turner, & Brooks, 2012). The relationship between PD and feature diversity is, however, still debated (Oliveira, Sheffers, & Costa, 2020; Tucker, Davies, Cadotte, & Pearse, 2018).

Methods emerging from Faith's PD include the Evolutionarily Distinct and Globally Endangered (EDGE) approach (Isaac, Turvey, Collen, Waterman, & Baillie, 2007). EDGE ranks species by combining their extinction risk with their evolutionary distinctiveness, determined from their position in a phylogenetic tree and number of close relatives. This approach has been applied to numerous animal groups (Gumbs, Gray, Wearn, & Owen, 2018; Isaac, Redding, Meredith, & Safi, 2012; Stein et al., 2018), but few plant groups and no fungi to date (Forest et al., 2018; Hills, Bachman, Forest, Moat, & Wilkin, 2019; Li, Gale, Kumar, Zhang, & Fischer, 2018; Yessoufou, Daru, Tafirei, Elansary, & Rampedì, 2017). Further metrics, inspired by EDGE, integrate evolution and extinction risks for conservation of species and areas (Farooq et al., 2020; Nunes, Turvey, & Rosindell, 2015; Pearse et al., 2015; Pimiento et al., 2020). Automation of such integrative analyses offers a dynamic approach, allowing rapid reevaluation of all available data, a powerful tool for more efficient and timely monitoring of biodiversity.

3.2 | Extinction debt and transient phenomena in plants and fungi

When an ecological community, such as a forest or wetland, suffers loss of area, extinctions likely follow. According to the *species-area relationship* (SAR, Box 2), if area falls so must the number of species (Halley, Sgardeli, & Monokrousos, 2013). However, the c. 600 modern plant extinctions reported (Humphreys et al., 2019) are much fewer than those predicted by the SAR (Cronk, 2016). One important reason is that extinctions are delayed. The community continues in a *supersaturated* state until the surplus, the *extinction debt*, is lost through a process of *relaxation* and a new *equilibrium* is established. Loss of natural habitat is the most frequently observed perturbation leading to an extinction debt (Figueiredo, Krauss, Steffan-Dewenter, & Sarmiento Cabral, 2019), although extinction debt can also arise through climate change (Malanson, 2008) or invasions (Downey & Richardson, 2016; Gilbert & Levine, 2013).

The observed *half-life* of the relaxation process ranges from weeks to thousands of years (Halley, Monokrousos, Mazaris, Newmark, & Vokou, 2016). This half-life increases with generation time, size of remaining area, and density of individuals. Half-life also varies with taxonomic group and species count. Several different theoretical mechanisms can model the delay of extinction (Hylander & Ehrlén, 2013). A biogeographical approach showed that in systems affected by a reduction in *connectivity*, species can persist for substantial time before their eventual *extirpation* (Tilman, May, Lehman, & Nowak, 1994). An alternative mechanism is observed in *neutral models*, where communities destined to lose species can continue for a time before a new equilibrium is established (Gilbert, Laurance, Leigh, & Nascimento, 2006).

Plants and fungi differ from most animals in undergoing potentially dormant stages (e.g., seeds or spores) and sometimes have great

BOX 2 A glossary for extinction debt

Colonization credit. Also called immigration credit. The species richness that a community can gain before arriving at the equilibrium specified by the species–area relation.

Coextinction. Loss or decline of a species due to loss or endangerment of (an)other species it depends on.

Delayed extinction. Extinctions that do not happen immediately after an event, but soon or long after the event.

Extinction debt. The species richness that a community must lose in order to reestablish an equilibrium consistent with the species–area relation.

Extinction. A species is considered extinct when no living individual of that species is known to survive.

Extirpation. Another word for *local extinction* (as opposed to *global extinction*) where an organism becomes extinct locally but not globally.

Functional extinction. An organism is functionally extinct when its abundance is so low as to be ecologically irrelevant to the community.

Half-life. The time taken after habitat loss (or other event) for a community to lose half of the extinction debt. Sometimes called *relaxation time*.

Imminent extinction. Extinctions that immediately follow an event, such as when all the habitat of an endemic species is destroyed.

Latent extinction risk. A measure of the potential for a species to become threatened. The difference, or discrepancy, between the current observed extinction risk of a species (e.g., in Red List) and the theoretical extinction risk predicted by its biological or population characteristics.

Relaxation. Local extinction of species in the community leading to reestablishment of an equilibrium consistent with the species–area relation.

Species–area relation or SAR. Equation relating the number of species a habitat can support to the area of that habitat. For example, the Arrhenius SAR has a power-law form: $S = bA^z$, where S is the species richness, A is the area, and b and z are constants.

Supersaturated community. A community for which the species richness is higher than can be sustained (i.e., $S > bA^z$), leading to extinction debt.

Time to first determined extinction. The time taken after loss of habitat (or another event) for the first extinction to happen as a direct result of that event.

longevity, which may further increase the relaxation time. Many studies examine extinction debt in plants (Halley, Monokrousos, Mazaris, & Vokou, 2017), most using inferential approaches, asking if “past landscape patterns explain current species richness better than the contemporary landscape pattern” (Cousins, 2009). Extinction debt studies

for fungi are few, reflecting major challenges: their cryptic nature, with mycelium hidden in the substrata, sometimes makes it difficult to define individuals; determining generation time is also problematic, but see Dahlberg and Mueller (2011). Obligate symbiotic fungi (i.e., mycorrhizas, endophytes, and parasites) likely experience a more complicated, and possibly two-stage extinction debt: first, the extinction debt from habitat loss or other direct impacts plus a confounding debt following extinction of their obligate plant partners.

Several studies suggest that *most* extinctions are delayed and, except in cases of extreme clustering, delayed extinctions could be orders of magnitude more numerous than immediate extinctions (Halley, Sgardeli, & Triantis, 2014). Since the half-life of relaxation may be thousands of years (Diamond, 1972), troubling questions arise about the extinction debt outstanding due to historical land use changes (Dullinger et al., 2013; Essl et al., 2011). The c. 600 plant extinctions of Humphreys et al. (2019) might be just the “tip of the iceberg”.

As long as extinctions have not happened yet, there is a window of opportunity to take appropriate action (Wearn, Reuman, & Ewers, 2012). For example, reintroducing threatened fungal species to suitable habitats within their historical range may turn extinction debt into species credit (Nordén et al., 2020). So, knowledge of extinction debt can be a motivation and means to design better conservation strategies (Newmark, Jenkins, Pimm, McNeally, & Halley, 2017).

3.3 | The drivers of plant and fungal extinction

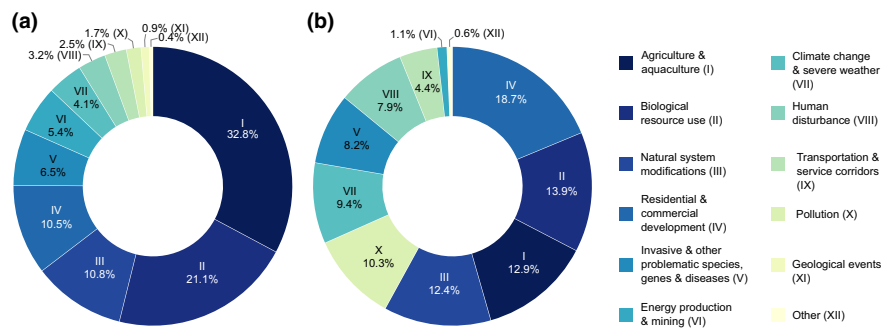
Globally and across all organismal groups, changes in land and sea use are considered the main drivers of biodiversity loss, followed by direct exploitation of organisms and climate change (Box 3; Díaz et al., 2019; RBG Kew, 2016). These drivers often interact synergistically (Bidartondo et al., 2018; Brook, Sodhi, & Bradshaw, 2008; Oliver & Morecroft, 2014) and in concert with other threats, such as pathogens, invasive species, and disruptions to ecological networks. As many fungi are obligate biotrophs of plants, plant extinction or the asynchronous migration between host and symbiont is likely to have a significant impact on fungal species loss (May et al., 2019).

3.3.1 | Land use change

Habitat loss due to agricultural expansion, urbanization, mining, and logging reduces population size and eventually causes extinction (Brook, Sodhi, & Ng, 2003). Current deforestation trends (FAO, 2016; Hansen et al., 2013) predict that land use change will remain a major driver of plant and fungal extinctions (Brinkmann et al., 2019; de Chazal & Rounsevell, 2009; Ichii, Molnár, Obura, Purvis, & Willis, 2019; Pereira, Navarro, & Martins, 2012). Loss of tropical forests alone is predicted to reduce the mature vegetation in biodiversity hotspots by 25%–60% between 2005 and 2100 (Jantz et al., 2015).

3.3.2 | Direct exploitation of species

Activities targeting particular species increase extinction risk for many plants and some fungi. These include selective logging, often

BOX 3 Overview of threats to plants and fungi**Breakdown of threats as categorized on the Red List for assessed (A) plant and (B) fungal species**

Despite rapid expansion of plant coverage over the past 3 years (2017–2019), the breakdown of threats based on the most recent Red List (IUCN, 2020a) closely resembles that from the 2015 Red List (RBG Kew, 2016). The top two threats remain agriculture and biological resource use while natural system modifications have overtaken residential and commercial development to occupy third place. These four threats collectively account for almost exactly the same proportion of threats reported for plants on the Red List as they did in 2015 (74.2% and 72.2%, respectively; RBG Kew, 2016). The proportion of all threats reported which relate to climate change and severe weather has also scarcely changed from 4.0 in 2015 to the current value 4.1%. This apparent stability appears contrary to our growing awareness of climate change as an important threat to plants (Willis, Ruhfel, Primack, Miller-Rushing, & Davis, 2008). It may be attributable in part to the timescales considered within IUCN assessments, as well as challenges inherent in documenting climate change threats to individual species (Trull, Böhm, & Carr, 2018). In contrast, the increasing availability of land cover data facilitates assessments citing threats associated with land use change, such as expansion or intensification of farming or residential and commercial development (Venter et al., 2016).

Habitat loss, especially due to expansion of residential areas, logging, and conversion of forests to plantations, represents the largest threat category for the fungi assessed to date, at approximately 62%. Impact of climate change is listed as a threat for 9.4% of assessed fungi. Climate impacts include both habitat shifting and changes in moisture, especially drought.

associated with illegal timber trade, firewood collection, or charcoal production; trade in medicinal plants and fungi and plants of high horticultural interest, including orchids and succulents; and hunting of seed dispersers. Deforestation facilitates access to previously remote populations of potentially exploited species, exacerbating exploitation (Brook et al., 2008; Haddad et al., 2015).

3.3.3 | Climate change

Empirical evidence for climate-driven global plant extinctions in recent centuries is very limited (Le Roux et al., 2019). However, several studies have attributed shifts in species ranges to increasing temperatures, which could eventually cause extinctions. For instance, in Ecuador's Chimborazo volcano, the upper limits of many mountain species have increased by c. 500 m on average over the last 210 years (Morueta-Holme et al., 2015). Similarly, in the Alps, many fungi were fruiting at significantly higher elevations in 2010 compared to 1960 (Diez et al., 2020). The disappearance of sensitive cyanolichens is a combined effect of climatic variables and pollution (Geiser & Neitlich, 2007). Controlled experiments show that climate change

is altering plant communities, particularly in boreal regions (Panetta, Stanton, & Harte, 2018; Reich et al., 2015). Modeling studies suggest increasing importance of climate change as a driver of plant extinctions later this century, with extinction impacts equaling or exceeding those of land use change in some regions (Gomes, Vieira, Salomão, & ter Steege, 2019). However, uncertainties relating to model choice (Araújo & Rahbek, 2006), complex species responses (Pimm, 2009), and future climate scenarios (Casajus et al., 2016) should be carefully considered. Declines of up to 50% in species' potential range sizes are predicted for this century (Gomes et al., 2019; Warren, Price, Graham, Forstnerhaeusler, & VanDerWal, 2018). These could suffice to evaluate almost half of all tree species as threatened following Red List criteria (Gomes et al., 2019; IUCN, 2012), in sharp contrast to the small fraction of current plant extinction risk assessments that report climate change as a threat (Box 3).

3.3.4 | Spatial variation

Land use change preferentially affects climate zones and plant habitats of most value for agriculture and human settlement, such as

humid climates and lowland and riparian habitats. In contrast, climate change affects the remotest plant and fungal communities, including those on mountains, hilltops, and steep slopes (Pimm, 2008; Pimm & Jenkins, 2019), hosting a disproportionately large fraction of the world's rare plant species (Enquist et al., 2019). Patterns vary between regions, with the Amazon Forest appearing more vulnerable to plant extinctions due to climate change than Brazil's Atlantic Forest (Silva, Rapini, Barbosa, & Torres, 2019). In general, narrow-ranged plant species face the greatest risks from multiple threats (Enquist et al., 2019; Newbold et al., 2018; Silva et al., 2019; Staude, Navarro, & Pereira, 2020).

4 | WHY INVEST IN EXTINCTION RISK ASSESSMENTS?

Despite their limitations in representing risks to species, extinction risk assessments remain among the most powerful tools in plant and fungal conservation science because they support and inform conservation policy, planning, and action. Guiding delineation and designation of protected areas, they influence allocation of NGO funding and private sector investment and thus they can prevent extinctions. Plants and fungi not on the Red List are overlooked in large-scale biodiversity studies and invisible to funding agencies. Underrepresentation of plants and fungi on the Red List limits options to promote their conservation.

Extinction risk assessments are central to recognizing Key Biodiversity Areas (IUCN, 2016) and Tropical Important Plant Areas (Darbyshire et al., 2017), international schemes with shared objectives of identifying areas with irreplaceable biodiversity. Updating and aligning their criteria (Darbyshire et al., 2017) have revitalized interest in pinpointing areas where plant diversity merits protection (e.g., Clubbe et al., 2020; Pearce et al., 2020).

In Europe, extinction risk assessments have been used for management and conservation of fungi since the 1990s (Dahlberg, Genney, & Heilmann-Clausen, 2010). Red List assessments, including National Red Lists, were used to define important fungus areas in the UK (e.g., waxcaps; Genney, Hale, Woods, & Wright, 2009), Austria (Fiala, 2014), and the US (Molina, Marcot, & Leshner, 2006).

As a global standard, the Red List is central to safeguarding/sustainability frameworks used by business and lenders (Bennun et al., 2018; Juffe-Bignoli et al., 2016). The International Finance Corporation (World Bank Group) requires clients to use the Red List to inform project risks and proscribes activities leading to net reduction in populations of CR or EN species. Thus, assessing species as CR or EN improves their survival prospects. Botanists found and assessed four threatened species (*Stylochaeton pilosus*, *Marsdenia exellii*, *Raphionacme caerulea* (all EN), and *Tarenna hutchinsonii* (CR)) on coastal inselbergs at Rio Tinto's (SIMFER SA) intended new port site at Senguelen, Guinea. Rio Tinto then amended construction plans to avoid these plants, and funded programs to bank seed and develop propagation protocols for them (Couch et al., 2014, 2019).

The development of robust, quantitative criteria has enabled the comparison of Red List status and trends (e.g., Red List Index; Butchart et al., 2007) between groups of organisms and regions. The Red List Index (RLI) has subsequently been recognized as an important indicator of biodiversity trends and is now embedded in global policy initiatives such as the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES, Díaz et al., 2019) and the United Nations Sustainable Development Goals (SDGs, Brooks et al., 2015).

5 | TRENDS IN EXTINCTION RISK IN PLANTS AND FUNGI

5.1 | Quantifying trends using the Red List Index (RLI)

The development of a RLI for fungi is challenging due to high levels of data deficiency (but see, e.g., Minter, 2020). For plants, a global RLI has been developed by taking a random sample of species from groups representing the geographical and taxonomic breadth of land plants (Brummitt, Bachman, Griffiths-Lee, et al., 2015). The baseline assessment found that, globally, one in five plants were threatened with extinction. Reassessment of the legume and monocot components of this global sampled RLI commenced in 2019. For this review, we analyzed 400 species occurring in Madagascar and Brazil, two megadiverse countries featured in earlier global overviews (RBG Kew, 2016, 2017). Our results (Figure 3a) are a subset of the global RLI and do not equate to any national or regional RLI (see 5.3).

5.2 | Trend estimation for selected megadiverse countries

Genuine changes in status may be conflated with increases in knowledge (see Box 4). To avoid this, we applied an approach that considered changes in area of occupancy (AOO) derived from land cover change maps spanning a 25-year period (see Methods S4; Santini et al., 2019; Tracewski et al., 2016).

Preliminary RLI values were generated from 400 sampled monocot and legume species occurring in Brazil and Madagascar (Figure 3a; Table S13). Without considering criterion B subcriteria, category changes were detected for three species, based on genuine changes in maximum AOO derived from area of habitat (AOH) calculations (Brooks et al., 2019). A slight decrease in RLI was detected for monocots and legumes, no change for Brazil, and the steepest downward trend for Madagascar. Decreasing RLI value indicates that species are moving toward extinction, a pattern consistent with other global RLIs, such as birds, mammals, and amphibians (Figure 3b). Position on the vertical axis indicates that legumes are less threatened than birds and monocots are less threatened than mammals. This contradicts the global SRLI value of 0.86 (Brummitt, Bachman, Griffiths-Lee, et al., 2015), which is likely lowered by the influence of extremely high levels of threat reported for the

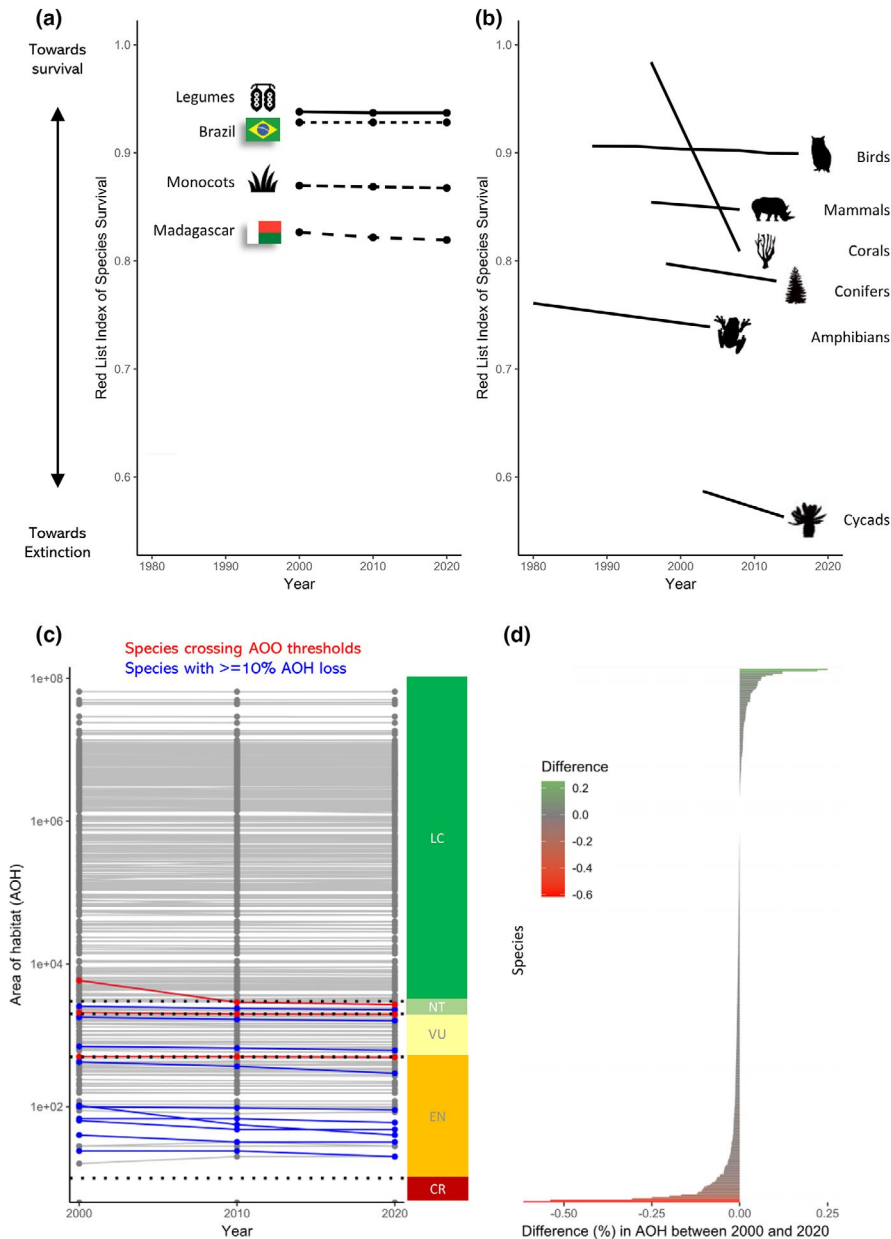


FIGURE 3 (a) The Red List Index of Species Survival for sampled species of monocot and legume occurring in Brazil and Madagascar. An RLI value of 1.0 (vertical axis) is equivalent to all species qualifying in the lowest threat category of Least Concern and an RLI value of 0 is equivalent to all species being Extinct. Monocots are more threatened than legumes, and species occurring in Madagascar are more threatened than species in Brazil. The speed of the trend toward extinction in Madagascar increased between 2010 and 2020. (b) Global RLI values for comprehensively assessed groups (IUCN, 2020a; from top to bottom: corals, birds, mammals, conifers, amphibians, and cycads) to provide context for sampled monocot and legume RLI values. (c) Area of habitat (AOH) for all species in the sample (grey lines) is reported for the years 2000, 2010, and 2020. Dotted lines and right-hand bar indicate thresholds for categories based on criterion B2 (AOO, area of occupancy). Red lines indicate when a species crossed a category threshold and blue lines indicate when a species lost $\geq 10\%$ of its range size between 2000 and 2020. Data for 2020 were projected based on trends in AOH derived from land cover change maps (1993–2018). (d) Difference calculated as percentage change in each species' AOH between 2000 and 2020. More species experienced a loss of AOH compared to those that gained, with a loss of $>60\%$ in one case

gymnosperms (including cycads and conifers). We show that of the 12 species that experienced range loss of $\geq 10\%$ between 2000 and 2020, only one triggered a change in category under criterion B2 (Figure 3c). The coarse nature of the Red List category thresholds means that large losses in occurrence, including from common species (Inger et al., 2015), may go undetected by the RLI (Figure 3d).

5.3 | Sub-global trends

Several studies have calculated RLI values and trends for plants at national level in Sweden, Finland, Spain, and South Africa (Gärdenfors, 2010; Juslén et al., 2016; Moreno-Saiz, Lozano, Gómez, & Baudet, 2015; Skowno, Raimondo, Poole, Fizzotti, &

BOX 4 Reassessments and genuine change

A species is not saddled with its Red List category for ever; it can deteriorate or improve in status and should be reassessed as new evidence is obtained. Conservation practitioners depend on the latest information to inform decision-making and therefore rely on an up-to-date Red List. Assessments on the Red List that were assessed using an older version of the categories and criteria (Oldfield, Lusty, & MacKinven, 1998) or assessments more than 10 years old are considered outdated (Rondinini, Di Marco, Visconti, Butchart, & Boitani, 2014); thus, 23% of Red List plant assessments currently require reassessment. In contrast, all but three published global fungal assessments are less than 6 years old. Pragmatism may be the main factor currently controlling reassessment priorities (e.g., see Methods S5), but a more strategic focus on reassessments will be important to ensure that the hard-won growth in assessment coverage is not eroded for want of an update. Reassessments are also important to the Red List Index (RLI) because the index is driven by genuine changes in status over time (Butchart et al., 2007). Difficulties arise when distinguishing genuine changes in status from increase in knowledge. Consider an isolated population documented after an initial assessment of Vulnerable. The apparent range extension triggers a reassessment of Near Threatened, and consequent improvement in the RLI, but this represents new knowledge of a population that was likely extant at the time of the first assessment. Avoiding potential errors of this kind will ensure that the Red List Index (5.1) reflects genuine changes in status and robust trends.

Slingsby, 2019). All showed comparable RLI values for plants of 0.87–0.9 and slight downward trends in RLI value where calculated. Despite calls to extend the RLI as a means of reporting at the national level (Bubb et al., 2009) and the importance of the sampled RLI approach to global indicators in the post-2020 framework (Díaz et al., 2019), implementation has proven challenging. However, recent analysis of sampled RLI behaviour suggests that trends in RLI could be detected with smaller, more manageable sample sizes of 200–400 species, although detecting changes in slope still requires at least 900 non-data deficient species (Henriques et al., 2020).

6 | ACCELERATING EXTINCTION RISK ASSESSMENTS

The challenge to complete species assessments more rapidly has stimulated the development of open access resources to facilitate or automate Red List assessment tasks. Packages developed for the

R programming language (R Core Team, 2019) include *rCAT* (Moat & Bachman, 2017), *redlistr* (Lee, Keith, Nicholson, & Murray, 2019), *ConR* (Dauby et al., 2017), and *red* (Cardoso, 2017), which calculate geographic range metrics from species occurrence data along with other useful parameters (e.g., estimates of fragmentation and sub-populations). The precursor of *rCAT*, *GeoCAT* (Bachman, Moat, Hill, de la Torre, & Scott, 2011), is a web app written specifically for extinction risk assessors to easily map species location data from multiple sources, and then calculate geographic range metrics.

Building on these tools and experience, approaches are emerging for rapid triage of species before assessment. For example, the Preliminary Automated Conservation Assessments approach (PACA; Stévar et al., 2019) builds on *ConR* to estimate different levels of conservation concern in order to identify likely threatened species for full Red List assessment. Other resources, for example Rapid Least Concern (Bachman, Walker, Barrios, Copeland, & Moat, 2020), focus on automated documentation and submission of Least Concern species to scale up assessment production. Artificial intelligence offers new opportunities (see Box 5) for rapid extinction risk estimation in large numbers of species, with application to relatively well-studied clades yielding promising performance (Darrah, Bland, Bachman, Clubbe, & Trias-Blasi, 2017; Nic Lughadha et al., 2019). A recent application attempted to generate predictions for all known plants (Pelletier, Carstens, Tank, Sullivan, & Espíndola, 2018) but produced more controversial results, prompting discussion of best practice for future studies (Walker, Leão, Bachman, Bolam, & Nic Lughadha, 2020).

7 | CONCLUSION

Plant and fungal biodiversity support all life on earth, meriting careful stewardship in an increasingly uncertain environment. Evaluating risks to both individual species and overall biodiversity is necessary to maximize species survival through prioritization and rational allocation of resources.

We reviewed qualitative and quantitative evidence to provide a critical overview of extinction risk estimates. While previous work estimated one in five (Brummitt, Bachman, Aletrari, et al., 2015) or 10%–62% (RBG Kew, 2016) of plant species are at risk of extinction, our predictions suggest that almost two in five known plant species may be threatened with extinction, even after correction for several known biases in species selection for assessment. However, other biases remain unquantified and may affect our estimate. Consideration of extinction debt and climate change suggests that the proportion of known species which are threatened may prove even greater. Furthermore, the many plant species yet to be described by science are likely to be small-ranged and highly threatened (Joppa, Roberts, Myers, & Pimm, 2011; Scheffers, Joppa, Pimm, & Laurance, 2012). Since these may number 50–100,000 (Corlett, 2016), the proportion of known species considered threatened can be expected to increase as plant species new to science are described at rates exceeding 2000 per year (Cheek et al., 2020) and assessed at an accelerated pace. As loss of some species may be inevitable, including some unknown

BOX 5 Horizon scan

Resource constraints have limited use of *genetics in plant species conservation* to individually tailored genetic marker studies in relatively well-resourced study systems (Clubbe et al., 2020). A low-cost genetic scorecard developed for wild species in Scotland is potentially broadly applicable (Hollingsworth et al., 2020). Fully harnessing the capacity of new sequencing platforms enables the next step: routine generation of large amounts of DNA sequence data from threatened species, offering direct measures of genetic diversity and insights into genome regions influencing individuals' survival prospects.

Environmental DNA (eDNA) sampling is now an important conservation tool (Thomsen & Willerslev, 2015). Sampling substrata (soil, wood, leaves, and roots) has great potential for documenting the presence of fungi even in the absence of visible spore bodies (e.g., mushrooms). Mycologists use eDNA to assess the potential conservation value of sites (Griffith, Cavalli, & Detheridge, 2019) and monitor, document, and model the distribution of taxa (Hao, Guillera-Aroita, May, Lahoz-Monfort, & Elith, 2020; Keepers et al., 2019; Suz et al., 2015).

Factoring climate change into plant species conservation is facilitated by ensemble approaches, increasing computing power, and cloud computing platforms (e.g., Google Earth Engine; Gorelick et al., 2017). The paucity of occurrence data for rare species presents a greater challenge, which may be ameliorated by the use of remotely sensed data (Baena, Boyd, & Moat, 2018; Zimmerman, Edwards, Moisen, Frescino, & Blackard, 2007).

The *IUCN Green List of Species* (renamed IUCN Green Status of Species) initiative developed metrics, for eventual integration in the Red List, to provide an optimistic vision of species conservation by evaluating species recovery in terms of geographic distribution, viability, and function (Akçakaya et al., 2018). Recent testing on plants highlighted challenges resulting from lack of baseline data. Also in development, the *Species Threat Abatement and Recovery metric* (STAR) quantifies potential for investments to reduce species extinction risk. Based on the Red List, STAR is scalable, additive, and more responsive to change than the Red List Index. A requirement for fully assessed groups limits its applicability to fungi and plants (CBD, 2019; IUCN, 2020b). *Continuous estimation of plant extinction risk* is achievable by 2025. A combination of remotely sensed land cover data that reflects threats and population trends (Tracewski et al., 2016), with new occurrence data from herbarium specimens and citizen science to update estimates of range size (Gardiner & Bachman, 2016; Long et al., 2019) and

BOX 5 (Continued)

artificial intelligence approaches to analysis, could yield extinction risk probabilities for each species (Walker, Leão, Bachman, Lucas, & Nic Lughadha, 2019).

to science, it is vital to understand how extinction risk is distributed across the tree of life; if it is concentrated in certain lineages, action can be directed to avoid losing all their evolutionary potential.

BOX 6 Fossil record

Although plants certainly respond to major environmental upheavals recorded in the fossil record (McElwain, Popa, Hesselbo, Haworth, & Surlyk, 2007), there is little evidence that they experience mass extinction on scales similar to animals (McElwain & Punyasena, 2007). Mass extinctions are commonly defined by the loss of at least 75% of animal species over a geologically short period of time (Barnosky et al., 2011), but studies on plants generally find negligible global extinctions (McElwain & Punyasena, 2007).

Plants have been considered more robust to the mass extinctions documented in the fossil record (e.g., driven by massive volcanic activity and/or bolide impact) due to their life-history traits, such as seed-dormancy, leaf-dropping, and hybridization (Traverse, 1988). Shifts in leaf-traits across mass extinction boundaries clearly show plant responses to these events, revealing traits associated with taxa that fared better across the end-Cretaceous extinction c. 66 mya (Blonder, Royer, Johnson, Miller, & Enquist, 2014) and the end-Triassic extinction c. 201 mya (Soh et al., 2017). However, doubt remains whether plants show clear evidence of mass extinction, even across the largest, the end-Permian mass extinction c. 252 mya. Recent studies support (Fielding et al., 2019) and refute (Nowak, Schneebeli-Hermann, & Kustatscher, 2019) an end-Permian plant mass extinction, but both record significant pressures on terrestrial ecosystems, and shifts in dominance and abundance in various plant groups. Ecosystem rearrangement (McElwain et al., 2007), therefore, appears to be a more common vegetation response to mass extinction events. Despite numerous gaps, the fossil record—the best accessible “long-term climate experiment”—shows plants as robust to previous mass extinction and major climatic upheaval events, being more likely to experience shifts in leaf-traits and dominance or abundance than major extinctions of many non-plant taxa. This makes the increasing numbers of threatened plant species in a modern context quite concerning.

While much evidence supports increasing estimates of extinction risk, documented global plant extinctions offer a slightly different perspective. The geographic distribution of modern extinctions broadly resembles that of plant extinction risk, but they are not clustered by evolutionary lineage. Moreover, modern rates (18–26 extinctions per million species years; Humphreys et al., 2019), although greater than background rates of plant extinction, are lower than equivalent estimates for animals. This pattern is consistent with the fossil record of mass extinctions (Box 6), although modern plant extinctions are likely underestimated due to extinction debt (3.2) and underreporting (Box 1).

Insufficient evidence is available to quantify global status or trends in fungal extinction risk, but a growing picture will develop as data from better studied regions and clades are consolidated. Evidence for global trends in plants supports a pattern of ongoing decline, although clades show considerable variation with extremes such as the highly threatened cycads and conifers.

Managing risks to plants and fungi requires updated extinction risk assessments for as many species as possible. Comprehensive up-to-date coverage by formal assessments seems unlikely for plants and impossible for fungi on timescales consistent with the urgency of the extinction crisis. However, novel artificial intelligence approaches show potential to deliver complementary best evidence extinction risk estimates for each species, regularly updated with observations from remote sensing and citizen science to rapidly respond to environmental change. These approaches could inform strategic development of the Red List by targeting species to add most value: species whose extinction risk prediction has greatest uncertainty; those where changing evidence suggests urgent need for reassessment; and most importantly, species most likely to be threatened—including those new to science—for which investment in a formal extinction risk assessment can increase survival prospects.

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AUTHOR CONTRIBUTIONS

E.N.L., S.P.B., T.L., and B.E.W. planned and designed the research; E.N.L., S.P.B., J.M., R.F.A.B., R.G., P.G.P.M., R.N., L.R., H.R., S.L.R., M.C.R., G.M.M., and B.E.W. undertook data collection, analysis,

and interpretation with critical technical input from A.C., J.I., G.P.L., E.C.S., and I.K.G. E.N.L., S.P.B., T.L., F.F., J.M.H., J.M., K.B., and B.E.W. wrote the first draft of the manuscript, incorporating contributions from C.A., G.G., S.C.G., P.H., P.R., E.J.L., J.M.O., A.A., and G.M.M. G.M.M. coordinated all mycological input. All authors provided comments and suggestion on a near-final version of the manuscript.

ORCID

Eimear Nic Lughadha  <https://orcid.org/0000-0002-8806-4345>

Steven P. Bachman  <https://orcid.org/0000-0003-1085-6075>

Justin Moat  <https://orcid.org/0000-0002-5513-3615>

Carmen Acedo  <https://orcid.org/0000-0001-6692-6509>

Karen L. Bacon  <https://orcid.org/0000-0002-8944-5107>

Ryan F. A. Brewer  <https://orcid.org/0000-0003-0369-2754>

Gildas Gâteblé  <https://orcid.org/0000-0003-2831-6384>

Susana C. Gonçalves  <https://orcid.org/0000-0001-6308-2662>

Paloma G. P. Moore  <https://orcid.org/0000-0003-3732-8029>

Raquel Negrão  <https://orcid.org/0000-0002-4758-8038>

Sophie L. Richards  <https://orcid.org/0000-0002-2466-2522>

Alexandre Antonelli  <https://orcid.org/0000-0003-1842-9297>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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