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REVIEW

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Plant and fungal collections: Current status, future perspectives

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Societal Impact Statement

Plant and fungal specimens provide the auditable evidence that a particular organism occurred at a particular place, and at a particular point in time, verifying past occurrence and distribution. They also document the aspects of human exploration and culture. Collectively specimens form a global asset with significant potential for new uses to help address societal and environmental challenges. Collections also serve as a platform to engage and educate a broad range of stakeholders from the academic to the public, strengthening engagement and understanding of plant and fungal diversity—the basis of life on Earth.

Summary

We provide a global review of the current state of plant and fungal collections including herbaria and fungaria, botanic gardens, fungal culture collections, and biobanks. The review focuses on the numbers of collections, major taxonomic group and species level coverage, geographical representation and the extent to which the data from collections are digitally accessible. We identify the major gaps in these collections

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and in digital data. We also consider what collection types need to be further developed to support research, such as environmental DNA and cryopreservation of desiccation-sensitive seeds. Around 31% of vascular plant species are represented in botanic gardens, and 17% of known fungal species are held in culture collections, both these living collections showing a bias toward northern temperate taxa. Only 21% of preserved collections are available via the Global Biodiversity Information Facility (GBIF) with Asia, central and north Africa and Amazonia being relatively under-represented. Supporting long-term collection facilities in biodiverse areas should be considered by governmental and international aid agencies, in addition to short-term project funding. Institutions should consider how best to speed up digitization of collections and to disseminate all data via aggregators such as GBIF, which will greatly facilitate use, research, and community curation to improve quality. There needs to be greater alignment between biodiversity informatics initiatives and standards to allow more comprehensive analysis of collections data and to facilitate linkage of extended information, facilitating broader use. Much can be achieved with greater coordination through existing initiatives and strengthening relationships with users.

KEYWORDS

botanical garden, culture collection, DNA and tissue Bank, fungarium, GBIF, herbarium, seed bank, specimen

1 | INTRODUCTION

Natural History collections are a unique resource for research using morphological and molecular techniques (Funk, 2018). They also provide evidence for research into conservation and to tackle broader societal challenges and are a resource for public education (Bakker et al., 2020; Kvaček et al., 2016). Each specimen represents a unique collection event. It is made up of the physical sample with its observable data and associated taxonomic, spatial and temporal information. Further data can be added including images, ecological information, and physical preparations (DNA sequences, slides, dissections) creating an "extended specimen" (Lendemer et al., 2020; Webster, 2017).

Digitization of collections increases specimen accessibility by making their metadata searchable through online portals. There is a shift from using the specimens alone to creating digitized products by increasing the type and amount of data linked to the specimen available for study, for example, via machine learning or citizen science (Hedrick et al., 2019). Consequently, new approaches in the use of collections have transformed the scientific landscape in areas such as conservation (Nic Lughadha et al., 2019), climate research (Johnson et al., 2011), and historic disease patterns (Harmon, Littlewood, & Wood, 2019). The use of collections as a "powerful research toolbox" (Bakker et al., 2020), creating innovative science, has been described extensively (Besnard et al., 2014; Carine et al., 2018; Funk, 2018; Heberling, Prather, & Tonsor, 2019; Meineke, Davis, & Davies, 2018; Nualart, Ibáñez, Soriano, & López-Pujol, 2017; Schindel & Cook, 2018; Soltis, 2017; Wen, Ickert-Bond, Appelhans, Dorr, & Funk, 2015). Several studies have focused on biases and gaps in collection data (Daru et al., 2018; Meineke et al., 2018; Meyer, Weigelt, & Kreft, 2016; Mounce, Smith, & Brockington, 2017) and, in addition, some biodiversity samples, such as desiccation intolerant seeds (Wyse, Dickie, & Willis, 2018) or environmental samples (Jarman, Berry, & Bunce, 2018) are difficult to store in current collections, limiting their research and conservation potential. A new era of interdisciplinary research on collections is influencing the future of collections and of collecting itself.

This article aims to provide a review of the current state of collections most relevant to plants and fungi to address the following questions: (a) What are the main taxonomic and geographical gaps in these collections? (a) To what extent are data from these collections digitally accessible? and (b) What new collection types are needed to support research and broader use? The review begins with the preserved collections of herbaria and fungaria, then living collections in botanic gardens and fungal culture collections, followed by seed and biobanks, and finally considers digitally accessible information from those collections. The above questions are addressed in the discussion.

2 | HERBARIA AND FUNGARIA

According to the data in *Index Herbariorum* (http://sweetgum.nybg.org/science/ih/), as of December 2019, there are 3,324 active herbaria in the world, containing 392,353,689 specimens

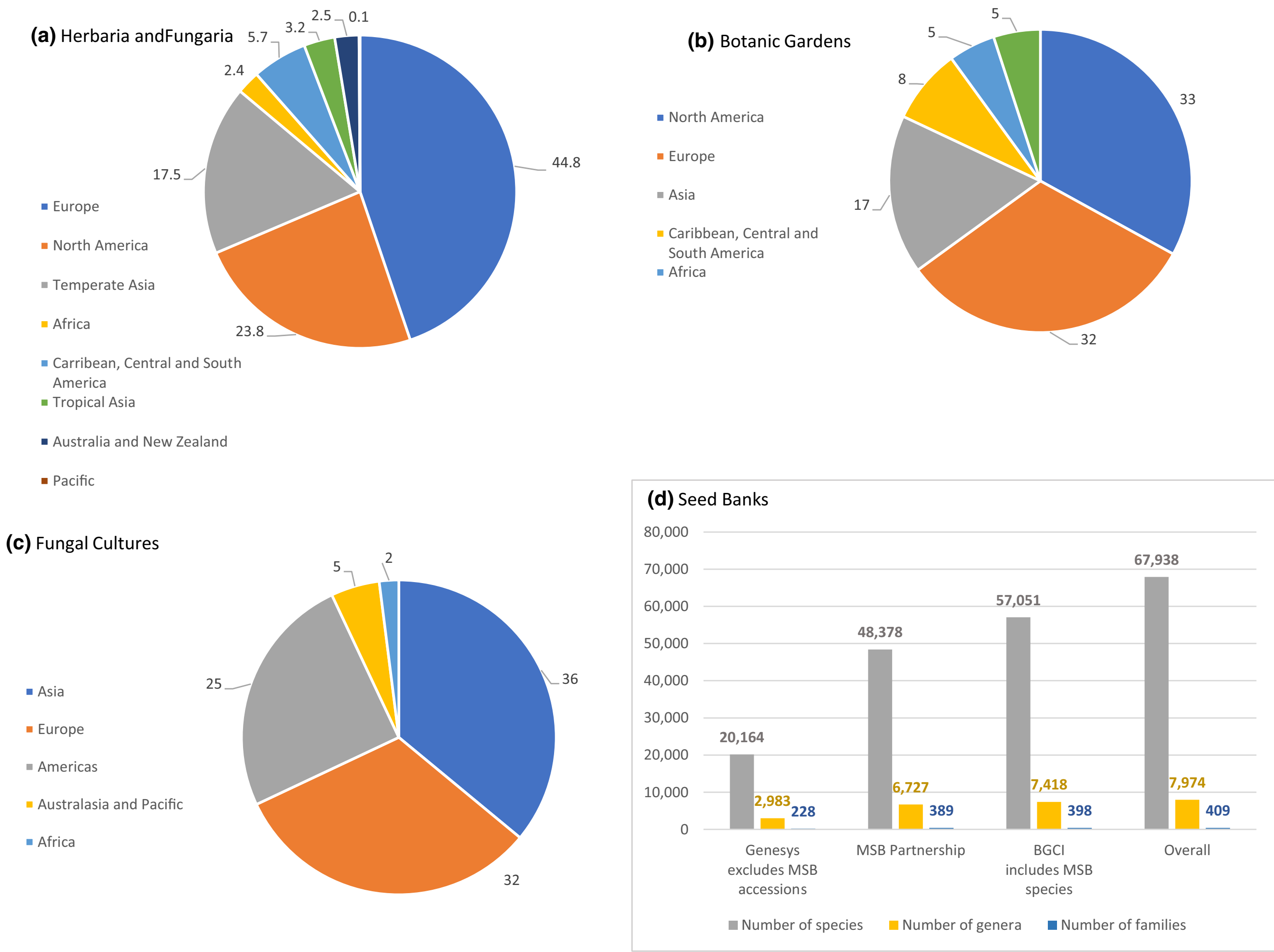

FIGURE 1 Representation of collections in different collection types. (a) A chart showing the proportion of herbarium specimens held in each continent (%). The total number of specimens recorded in Index Herbariorum is 392,353,689; (b) a chart showing the proportion of Botanic Gardens collections held in each continent (%). For institutions listed in GardenSearch, 32% of have provided collection data to BGCI's PlantSearch, which presently includes 1,471,901 records representing 107,304 accepted species. The source of data in PlantSearch largely matches that of the location of the collections, most data coming from collections in Europe and North America; (c) a chart showing the proportion of microbial culture collections held in each continent (%) as recorded by WDCM; and (d) the results of a survey of the representation of both crop and wild seed plant taxa in the form of seeds in ex situ storage (short-, medium-, or/and long-term storage, including cryopreservation) at institutes across the world; including genebanks, seed banks, and botanic gardens. It is a compilation of separate, but overlapping species lists from: (i) the MSB itself plus collections elsewhere within the MSB Partnership, but not duplicated at the MSB; (ii) in seedbanks worldwide using records from PlantSearch; and (iii) elsewhere in genebanks worldwide, using accessions recorded on the GENESYS-PGR, the global online portal for Plant Genetic Resources for Food and Agriculture

(Thiers, 2020). There are 178 countries with at least one herbarium (Thiers, 2020). *Index Herbariorum* organizes herbaria into regions following Brummitt, Pando, Hollis, and Brummitt (2001) except that Russia and former members of the Soviet Union are all included under Temperate Asia. North America (Canada, Greenland, Mexico and the United States) has the most, with 844 herbaria. Europe, with only slightly fewer herbaria (828) has by far the largest number of specimens—nearly 45% of all the world's herbarium specimens are found in European herbaria (Figure 1a). The large specimen total for Europe reflects the European origin of the herbarium tradition and the fact that European herbaria hold many specimens from outside Europe gathered during the colonial expeditions of the 17th to 19th centuries. Temperate Asia, which includes both Russia and China, ranks third in terms of the number of herbaria and specimens, but has more staff associated with herbaria than either Europe or North America. The ratio of specimen total to the number of staff may serve as a proxy for the level of research and curation activity in regional herbaria. These ratios range from 1.6 staff per 100,000 specimens in Europe to a high of 11 staff per 100,000 specimens in the Pacific region. Some botanically diverse areas have few herbaria: the island of New Guinea has five herbaria, and a vascular plant flora of 13,634 species (Cámara-Leret *et al*., 2020), compared to the UK with 223 herbaria and vascular plant flora of around 7,400 native and naturalized species (BSBI, 2020).

Only a small proportion of herbaria in *Index Herbariorum* have provided information of their holdings by taxonomic groups: that is, how many specimens held, how many databased and imaged, for seed plants, algae, bryophytes, ferns, and related groups and fungi. As a result, these data are still too provisional to be of use, and as discussed later, this restricts understanding of collection gaps and what still needs to be digitized.

3 | PLANT COLLECTIONS IN BOTANIC GARDENS

Botanic Gardens Conservation International (BGCI) maintains a global database of botanic gardens and associated institutions (*GardenSearch*, https://tools.bgci.org/garden_search.php). This currently includes records for 2,991 botanic gardens, 97 gene/seedbanks, 99 zoological institutions, 21 private collections and 436 "other" institutions covering 182 countries. These collections are located largely in North America (33%) and Europe (32%) (see Figure 1b). The holdings of botanic gardens worldwide were recently reviewed using data from BGCI's *PlantSearch* (https://bgci.org/resources/bgci-databases/plantsearch/; Mounce et al., 2017). Since the data used for that analysis were extracted (November, 2015), 10% more collection records (increasing taxon records by 20%) have been added to the *PlantSearch* database, largely from China, Mexico, and Brazil. A reanalysis of the *PlantSearch* database suggests 107,340 accepted species are represented in botanic gardens collections, representing 31% of vascular plant species (WCVP, 2020). In comparison with the BGCI *ThreatSearch* (https://tools.bgci.org/threat_search.php) database, 35% of known threatened species are represented in *PlantSearch*.

Species diversity in botanic gardens is latitudinally biased, increasing in temperate latitudes. Mounce et al. (2017) note that 93% of species in the botanic garden network are held in northern temperate institutions. They also note that tropical species are poorly represented, suggesting that a temperate species has a 60% probability of cultivation in the botanic garden network, whereas this is just 25% for a tropical species. There are also phylogenetic biases in botanical garden collections; bryophytes and several vascular plant lineages with clusters of tropical genera are unrepresented in these living collections.

4 | FUNGAL CULTURE COLLECTIONS

Fungal cultures held in international microbial Biological Resource Centres underpin research and development and the global bioeconomy. These centers are well placed to strengthen infrastructure to aid governments as they strive to deliver their commitments to the United Nations' sustainable development goals (Antonelli, Smith, & Simmonds, 2019). However, to achieve this objective, they must not only consolidate their existing capacities but also evolve their approaches to meet the ever-changing requirements of their users (Ryan, McCluskey, Verkleij, Robert, & Smith, 2019).

The World Data Centre for Microorganisms (WDCM) provides a global view of microorganisms that are held and available from the microbial resource centres registered with them. They make almost 3.2 million strains of microbes available for reference and research; of these 849,724 are fungal strains. The data are extracted from 793 culture collections in 77 countries and regions (Figure 1c). However, these collections represent the existing fungal diversity rather poorly (Overmann & Smith, 2017). The collections and strains are distributed disproportionately with most in Europe (250 collections), and North America (197 collections). Africa is one of the megadiverse regions of the world yet only has 18 collections.

There are over 148,000 fungal species described currently (Species Fungorum, 2020). However, estimates based on high-throughput sequencing methods suggest that as

BOX 1 The Millennium Seed Bank

The Millennium Seed Bank (MSB) is the world's most diverse wild species seed bank: of the total number of species estimated to be represented in ex situ seed collections worldwide, over 70 percent are held at the Millennium Seed Bank (MSB, https://www.kew.org/science/collections-and-resources/collections/seed-collection), or in its partner institutes (the MSB Partnership –MSBP, http://brahmsonline.kew.org/msbp/SeedData/DW; Figure 2a,b). The conservation value of MSB collections, both qualitative and quantitative, was reviewed in depth by Liu, Breman, Cossu, and Kenney (2018).

The inclusion of ferns and lycophytes in Figure 2a demonstrates that the spores of many can be successfully conserved like orthodox seeds. There is at least one substantial conservation collection of fern spores; at the Royal Botanic Gardens Edinburgh, where 1,570 spore collections of 38 families, 134 genera, and 488 species of ferns are currently kept air-dry in deep-freeze and refrigerators (S. Barber, pers. comm.). There is also evidence that at least some fungal spores and pollen can be conserved like orthodox seeds (Hong et al., 1999; Hong, Jenkins, Ellis, & Moore, 1998).

Among the MSB's collections around 10% of species and their infraspecific taxa, representing over 8% of collections, are either extinct in the wild, rare, or threatened at the global and/or national level. Furthermore, around 20% of taxa, represented in some 13% of collections, are endemic at the country or territory level. Tropical Asia, Southern America and The Pacific are under-represented. Africa, (including Madagascar) which is comparatively well-represented, has been a focus for the MSB Partnership over many years.

many as 2.2–3.8 million fungal species are estimated to exist (Hawksworth & Lücking, 2017), most of which are yet to be described and cultured. At least in part, the failure to recover phylogenetically novel fungi can be attributed to the current isolation methodology that results in quick-growing, common fungal species dominating isolation programmes. It is essential that the rarely isolated organisms are deposited in collections to ensure that they are available for study. However, only 25,611 species (Global Catalogue of Microorganisms, 2020), just over 17% of those described, are cultured and publicly available. Innovations in advanced cooling technology are facilitating methodologies to preserve non-culturable fungi. This is an exciting area of developing research associated with the need to develop infrastructure to support the microbiome research community (Bell, 2019; Ryan et al., 2019).

A significant proportion of microbial diversity remains undescribed although visible through genomic studies. The UNITE database provides a sequence management environment for the molecular identification of fungi. Sequences are clustered into species hypothesis and assigned unique identifiers to allow unambiguous reference (Nilsson et al., 2019). Many studies sampling fungal diversity in under-explored environments have shown that they contain species new to science. In the tropics, Ritter et al., (2020) recently showed that a single teaspoon of Amazonian soil may contain as many as 400 Operational Taxonomic Units of fungi, roughly equivalent to genetically separate species. But undescribed species are also found in temperate and glacial regions, as recently shown by the study surveying 130 locations in Denmark in which over 100 new species of fungi were described (Velux Foundation, 2020) and new discoveries from the Antarctic Peninsula (Ogaki et al., 2020).

5 | SEED BANKING

Seed banks were originally developed as a cost-effective means of ex situ conservation of plant diversity, to mitigate the anticipated loss of genetic resources from the world's major crops (Li & Pritchard, 2009). Of the more than 1,750 agricultural seed banks worldwide, most focus on species currently covered by the International Treaty on Plant Genetic Resources for Food and Agriculture (Hay & Probert, 2013). The status of those collections is well documented elsewhere (Bélanger & Pilling, 2019; The Crop Trust, 2019). More than 4.9 million accessions from over 6,900 genera are conserved under medium- or long-term conditions in 90 countries and 16 international/regional centers, including around 1 million collections duplicated in long-term storage in the Svalbard Global Seed Vault, Norway.

Although the International Treaty on Plant Genetic Resources covers 64 seed plant crops, there are an estimated 331,000 species of seed plants (WCVP, 2020). Around 10% globally are estimated to bear seeds that cannot be preserved successfully in conventional seed banks (Wyse & Dickie, 2017). However, individual crop seed banks also store collections of wild species, especially the close wild relatives of their crops of interest; but also conservation collections of a wider range of wild taxa. For example, the United States Department of Agriculture (USDA) National Plant Germplasm System Collection currently conserves 13,429 plant species (USDA Agricultural Research Service, 2017).

The Convention on Biological Diversity commits signatories to ex situ, as well as in situ biodiversity conservation; made more explicit in the Global Strategy for Plant Conservation Target 8, which calls for "at least 75% of threatened plant species in ex situ collections, preferably in the country of origin." This target has driven significant

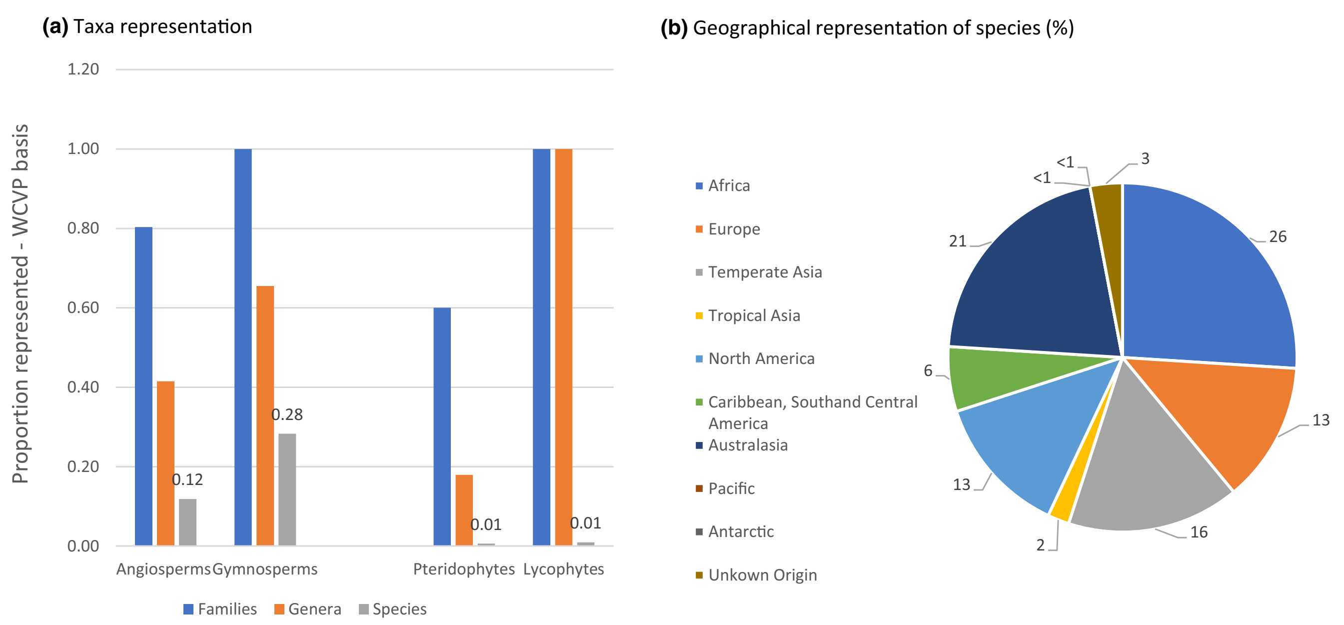

FIGURE 2 (a) A chart depicting the proportional representation of taxa in the MSB collection; and (b) a chart presenting the geographic representation of species in the MSB collection (%)

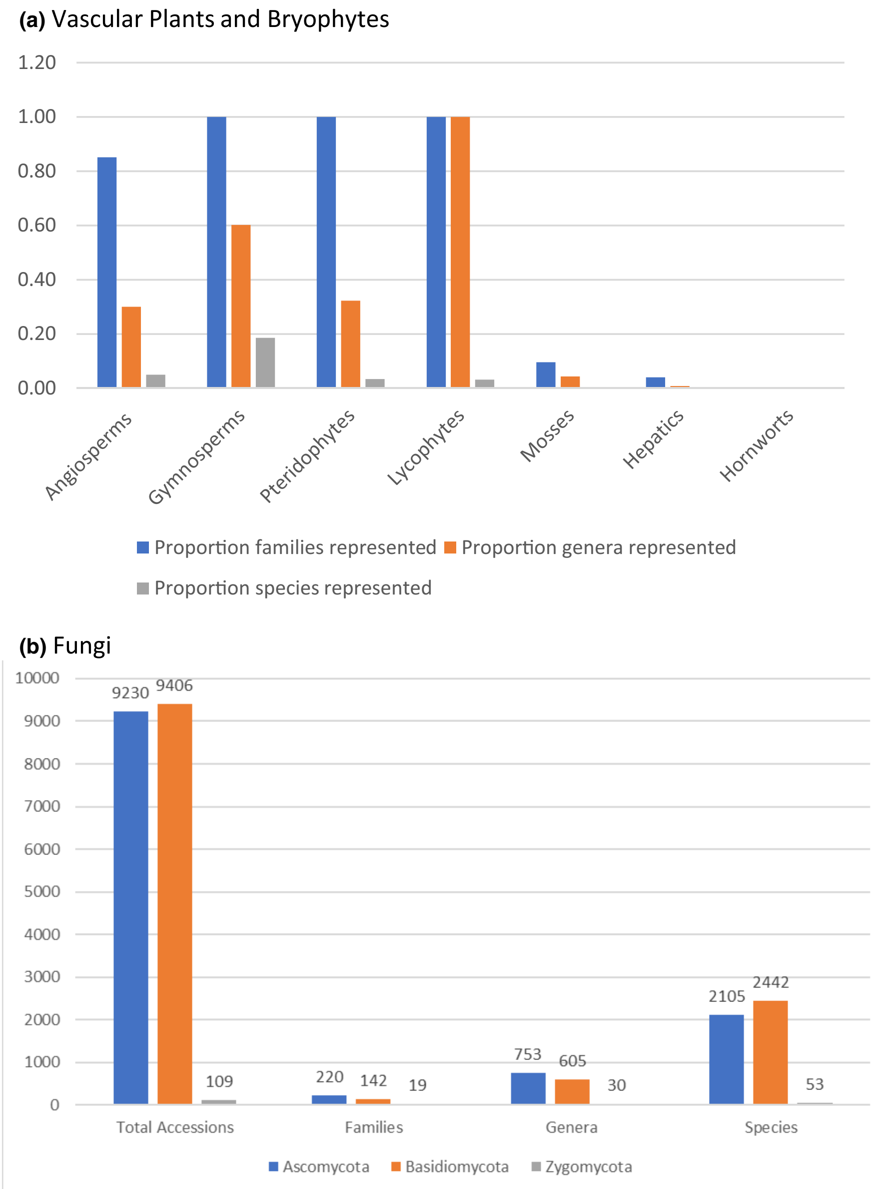

FIGURE 3 Taxonomic representation in the GGBN database. (a) A chart of vascular plant and bryophyte taxon representation of collections; (b) a chart of Fungi taxon representation of collections. Chytridiomycota and Glomeromycota are not represented in the GGBN. There are only 109 accessions of Zygomycota representing 53 species

growth in the number of ex situ seed conservation facilities for wild species (Figure 1d). Botanic gardens make a significant contribution to ex situ conservation of wild species (Mounce et al., 2017), including through seed banking. O'Donnell and Sharrock (2017) found that there are at least 350 seed banking botanic gardens in 74 countries. In total 57,051 species (17% of seed plants) have been banked including more than 9,000 taxa that are threatened with extinction; and 6,881 tree species, more than half of which are single country endemics and represent species from more than 166 countries.

Major seed banks index their collections using different standard taxonomies. Thus collections of the same species may be catalogued under different accepted names. While GENESYS-PGR (https://www.genesys-pgr.org/; Figure 1d) relies heavily on names supplied by contributors; *PlantSearch* heavily, but not exclusively on the "static" Plant List; names in the Millennium Seed Bank (MSB) and Partner collections are checked dynamically against the World Checklist of Vascular Plants (WCVP, 2020). The inconsistent application of names is more of an issue for analysis of seed collection data than for fungal culture or botanic gardens as there are no single resource holding data from all seedbanks and managing these inconsistencies. Furthermore, some species listed are known or strongly suspected of bearing seeds that will not survive storage in a conventional seed bank ("recalcitrant"—Wyse & Dickie, 2017). Hence, further analysis is restricted to a single, diverse collection: that at the MSB (Box 1).

6 | DNA AND TISSUE BIOBANKS

The molecular revolution in plant and fungal science has driven a dramatic increase in the demand for the availability of biological samples of sufficient quality for genomic research. To satisfy this demand biodiversity repositories and institutes have increasingly developed dedicated biobanks for preserving both tissue material (usually leaves in plants; fruiting bodies in fungi) and extracted DNA. The Global Genome Biodiversity Network (GGBN; Seberg et al., 2016) coordinates this activity for non-human organisms across a network of institutions, providing an infrastructure for the global effort to sample the Tree of Life. It focuses on both sample quality management and data integration and sharing, as well as facilitating the prioritization of new sampling.

The GGBN Data Portal (http://data.ggbn.org/ggbn_portal/) gives on-line access to genome-quality samples and data from across the network. While the proportional representation of various plant and fungal groups is likely to be reasonably accurate, the absolute numbers of collections in those groups are almost certainly underestimated because of the relatively recent expansion of DNA and tissue banking of plant and fungal groups. New members are regularly joining GGBN and there are more collections in existence than currently recorded. Many member organizations hold significant numbers of collections that have not yet been databased to GGBN standards, mostly due to insufficient resources. Representation of non-seed plants at the species level is very approximately 10-fold lower than that of seed plants, with hornworts not represented at all (Figure 3a). In fungal groups collections are dominated by Ascomycetes and Basidiomycetes (Figure 3b). We did not analyze the geographic origins of the collections as the current goal of GGBN is to achieve a wide taxonomic representation, rather than in-depth geographical coverage, hence only a few taxa are represented from more than one country.

7 | DIGITALLY ACCESSIBLE DATA

There has been a huge increase in the mobilization and use of digital collections data (Lendemer et al., 2020; Nelson & Ellis, 2019; Schindel & Cook, 2018) with the role of data aggregators such as the Global Biodiversity Information Facility (GBIF) on the global scale (GBIF, 2019a) and national and regional initiatives such as Atlas of Living Australia (https://www.ala.org.au/about-ala/), iDigBio (Soltis, 2017), Brazil's Reflora Virtual Herbarium (Canteiro et al., 2019) and Brazil's GBIF node (https://sibbr.gov.br) all being important infrastructures supporting data accessibility. Figure 4a shows the broad application of GBIF mediated data in scientific publications. In 2015, GBIF initiated a DOI-based protocol for citation of data downloaded through gbif.org. To date this effort has linked nearly 2,500 peer-reviewed research articles to data providers in the GBIF network, including herbaria and botanic gardens. In 2019, 744 peer-reviewed articles cited GBIF data, over two per day. The digital accessibility is critical for the broad range of use and the subsequent value it gives back to providing herbaria. Citations inform funders

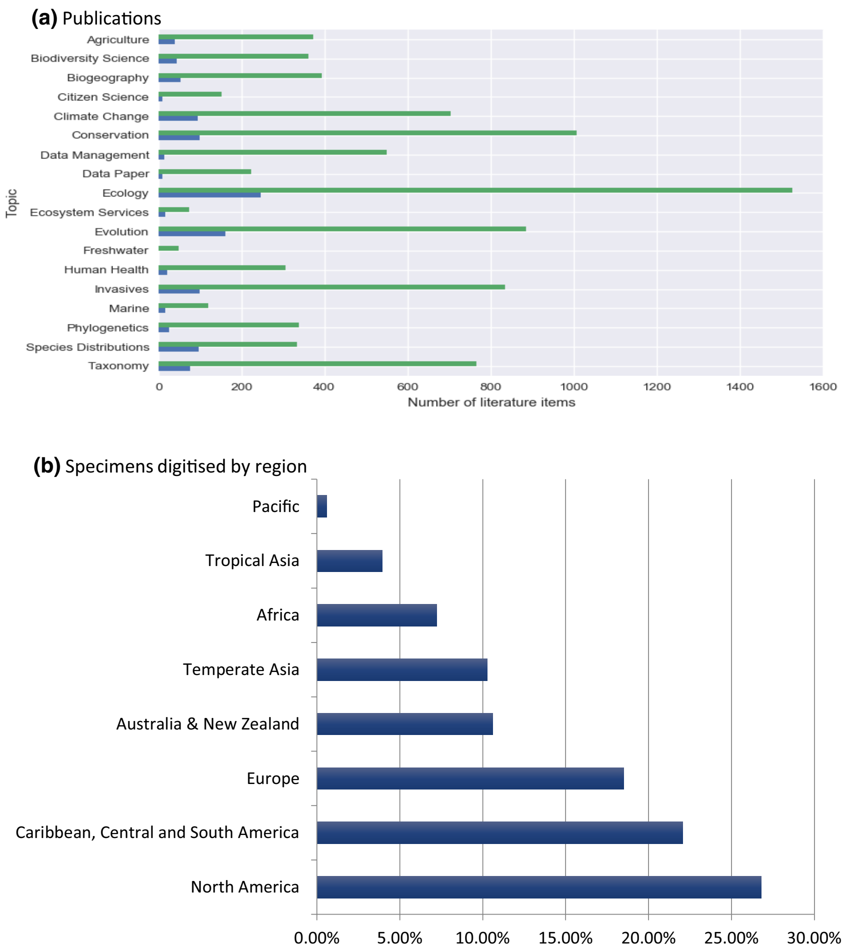

FIGURE 4 Citations and geographic representation of specimen data available via GBIF. (a) A chart showing the number of papers citing GBIF (green) or downloads using GBIF-minted DOIs (blue) across different science disciplines. The data used results from a call to the GBIF resource API to gather bibliographic items citing GBIF or GBIF mobilized datasets, monitored through the GBIF literature tracking service (GBIF, 2020). The dataset contains 9,018 records. Literature citing GBIF mediated data were grouped by topic and subdivided into those which directly cited a specific GBIF-mediated download (labeled with a dataset download DOI) and those which cited the GBIF data portal generally; (b) percentage of specimens digitized by region. The digitization statistics were derived from a search of GBIF (www.gbif.org, accessed 26 Jan 2020). Note that these numbers reflect the number of specimens digitized from the region, not necessarily the digitization efforts in those regions

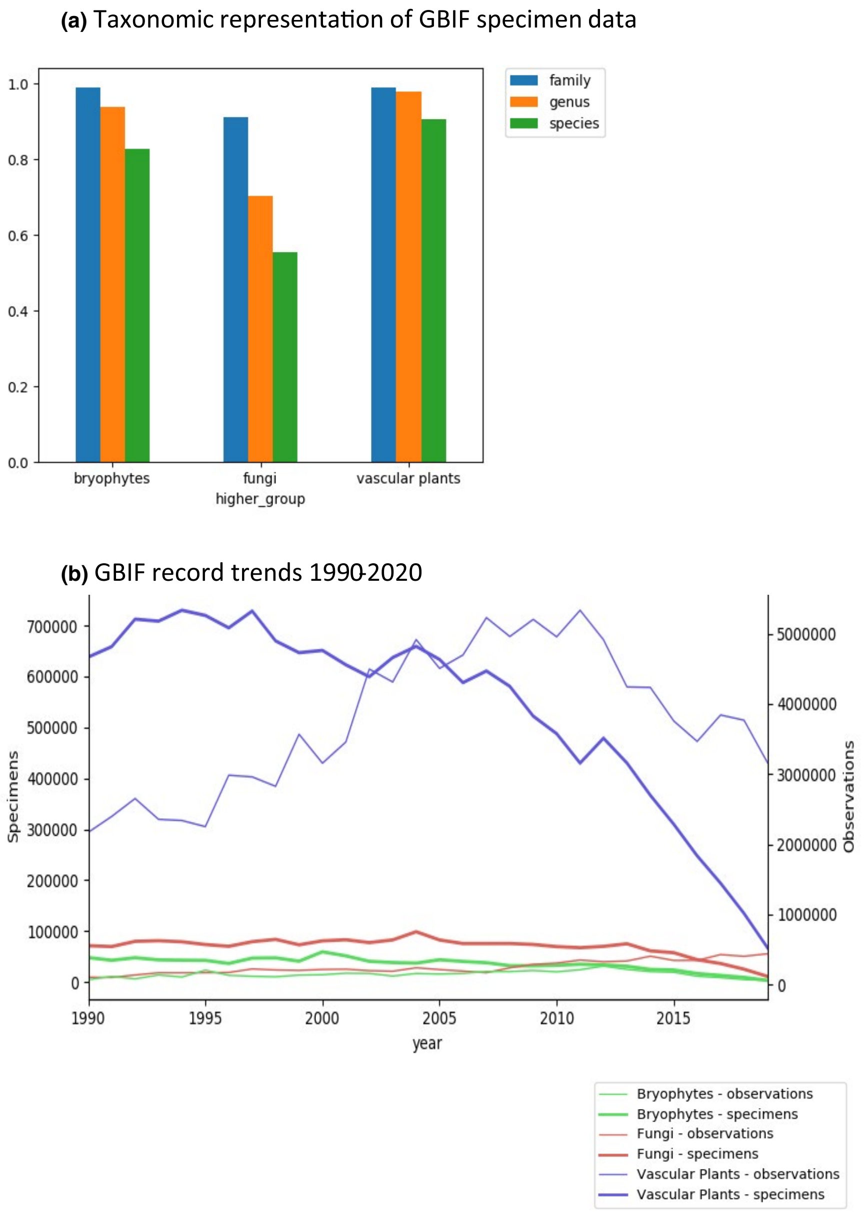

FIGURE 5 Taxonomic representation and yearly addition of specimen and observation data in GBIF. (a) Taxonomic representation of GBIF specimen data of different ranks of major groups compared with the GBIF taxonomic backbone (GBIF, 2019c). (b) Charts for fungi, bryophytes, and vascular plants; each showing the total number of preserved specimens and observations/year in GBIF for the date range 1990–2020

of the collections importance by directly connecting herbaria data to global research and policy (e.g., Díaz et al., 2020; IPCC, 2018). It is worth noting that publication citation metrics alone only partially reflect breadth of use of collections. Tracking the use of specimen persistent identifiers and encouraging their citation would provide a more complete picture of the use and value of collections (McDade et al., 2011).

Despite the success of these data aggregation initiatives, much remains to be digitized. There are data from 85,576,113 preserved specimens of plants and fungi represented in GBIF, only around 21% of all herbarium specimens; and only 48% of those have coordinate information. The largest proportion of digitized specimens are from North America; Africa, Tropical Asia, and the Pacific (excluding Australia and New Zealand) regions comprise the smallest proportion of digitized specimens currently available through GBIF (Figure 4b). It is worth noting that most large-scale digitization projects to date have taken place in relatively well-funded collections. This has left behind many small herbaria in biodiverse countries that often contain a rich representation of the local flora, including irreplaceable singletons (species that could only provide a single herbarium specimen and therefore are sometimes required by law to stay within the country). As those herbaria are often under-resourced, they run increased risks of damage by pests, fire, and other hazards.

7.1 | Taxonomic coverage and data mobilization

There are taxonomic, spatial and temporal biases, uncertainties and errors related to the data already mobilized (Daru et al., 2018; Meineke et al., 2018; Meyer et al., 2016; Nekola, Hutchins, Schofield, Najev, & Perez, 2019; Zizka, Antonelli, & Silvestro, 2020). In order

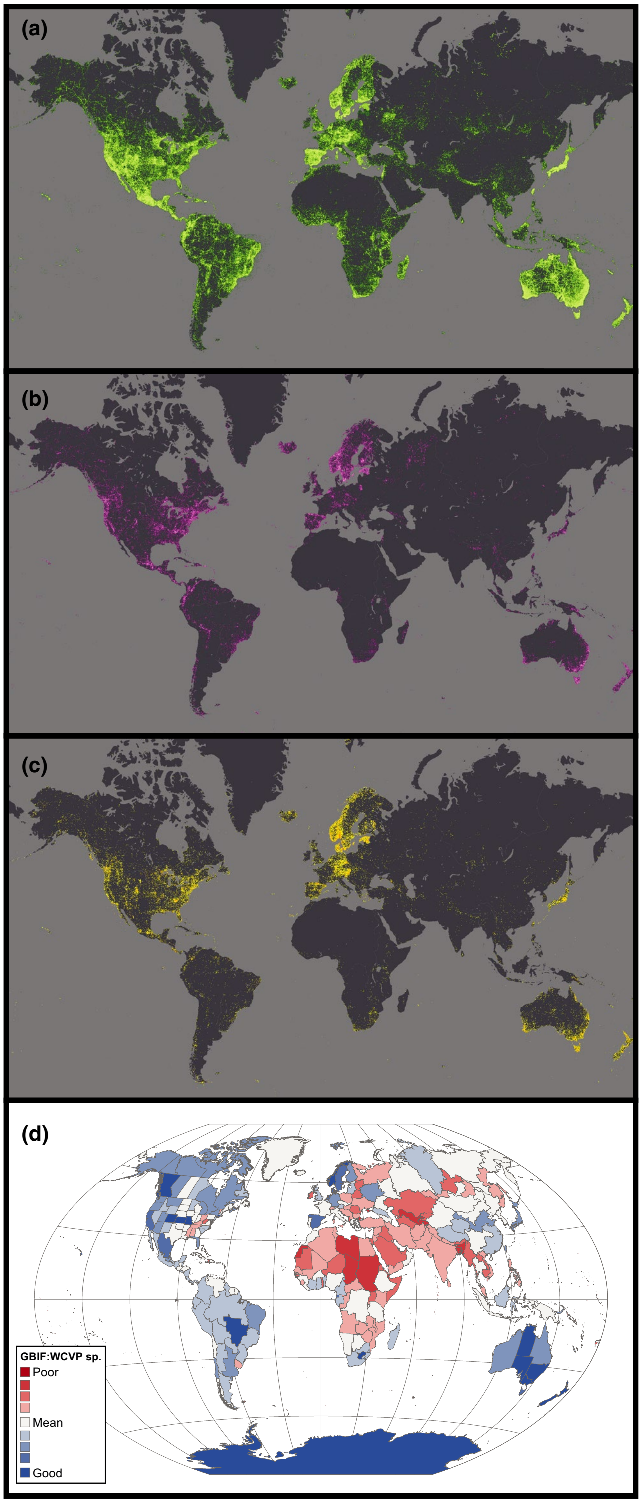

FIGURE 6 Point distribution of specimen occurrence and species representation of plant and fungal specimen data in GBIF. Point distribution of (a) Vascular Plants; (b) Fungi; and (c) Bryophytes. GBIF maps were downloaded using leaflet (Cheng, Karambelkar, & Xie, 2019) in R (R Core Team, 2019) using the GBIF maps API (https://www.gbif.org/developer/maps). Vascular plants, fungi, and bryophytes were queried using taxonid and for preserved specimens only; (d) Ratio of species present in GBIF data compared to reported species at World Geographical Scheme for Recording Plant Distributions (WGSRPD) level 3 areas (Brummitt et al., 2001) from WCVP (2020), shows a mean ratio of 0.82 of the total species that we believe should be in each WGSRPD level 3 area according to WCVP. Areas in dark red are where the total number of species is relatively poorly represented by GBIF coverage, in dark blue the total number of species show relatively good representation. WCVP data are likely to under-represent the presence of non-native species thus ratios are likely to be inflated

to explore the taxonomic biases, we considered coverage of vascular plants, bryophytes, and fungi at different taxonomic ranks (Figure 5a). While 90% of species of vascular plants and 82% of bryophyte species are represented in GBIF data (GBIF, 2019b, 2019c), only 55% of fungal species are represented. Calculating the accumulation of specimens by species shows that 95% of GBIF data on fungi represents only 26% of species; 24% of bryophytes; and 38% of vascular plant species.

Meyer, Kreft, Guralnick, and Jetz (2015), Meyer et al. (2016) and Heberling and Isaac (2018) note that there is a significant delay in making digital specimen records accessible. Figure 5b shows that vascular plant and, to a lesser extent, fungal specimens are accumulating in GBIF slowly after 2012, in comparison to records available for dates prior to that; and more slowly than observation records.

7.2 | Spatial coverage

Meyer et al. (2016) reported that although absolute numbers of unrecorded species were highest in the tropics there was not a "tropical data gap" in the pattern of proportional taxonomic coverage. These authors noted that some emerging economies are even more under-represented regarding digitally accessible information than species-rich, low-income countries in the tropics. These authors did record relative gaps across most of Asia, Northern and Central Africa, Amazonia and Arctic Canada. We examined species distribution in GBIF vascular plant specimen data and compared this to the distributions of vascular plants recorded in WCVP (2020). The relatively under-recorded areas are broadly consistent with those reported by Meyer et al. (2016) (Figure 6a–d).

8 | DISCUSSION

8.1 | What are the main taxonomic and geographical collection gaps?

Around 31% of vascular plant species are represented in botanic gardens, and 17% of known fungi species held in culture collections. These living collections are geographically biased toward collections in Europe and North America and Asia for fungal cultures. Wild seed banks and plant and fungal biobanks are relatively recent and cover a relatively smaller proportion of species (Figures 1d and 3). Taxonomic and geographic diversity of non-digitized herbaria and

BOX 2 Addressing collection gaps in the Karoo, South Africa

The plant and fungal diversity in large areas of South Africa remain poorly explored (Victor, Smith, Wyk, & Ribeiro, 2015). One such area is the Karoo, a biodiverse but poorly delimited region that has been earmarked for shale gas exploration, as well as the Square Kilometre Array radio telescope development. The South African National Biodiversity Institute initiated and led a project to fill biodiversity information gaps, thus providing support for decision-making regarding development and conservation management in the Karoo. Efforts from a collaborative network made up of a consortium of over 20 non-governmental organizations, universities, science councils, and collections institutions, among others, have resulted in an increased number of specimens representing these poorly known areas in herbaria, the description of new plant and fungal species and the collation of additional foundational biodiversity information such as extensions of distribution ranges, revision and updating of taxonomic concepts, and more comprehensive information about existing plants and fungi in the Karoo. This information was used for the Strategic Environmental Assessment of the Karoo area to highlight the sensitive areas that should not be developed. Furthermore, it has also been incorporated into a government department's Environmental Impact Assessment screening tool, a decision support tool that has been legislated for use during environmental authorization processes.

BOX 3 National level support for collections

The Natural Science Collections Facility (NSCF) of South Africa is a virtual facility comprising a network of 14 natural science collections institutions, including museums, herbaria, science councils and universities (www.nscf.co.za). The purpose of the NSCF is to promote and upgrade natural science collections, making the collections and their associated data accessible for research. The NSCF, launched in October 2017, is funded through a governmental grant allocated to improving South Africa's research infrastructure. NSCF funds are used to invest into improving specimen storage facilities, improving human capacity and resources for care of collections, upgrading research equipment, and digitizing and harvesting data for dissemination to the public.
Outputs expected from the NSCF include publications produced by researchers using the collections; increased capacity for caring for collections through training and development of manuals and policies; new species described; improved collaboration and networking; increased numbers of scientists visiting collections for research purposes; increased numbers of specimens sent out on loan; improved ability to do identifications; capturing and digitization of specimen label information; development and improvement of databases for disseminating data; and generating postgraduate students using collections for their research.
The NSCF has brought together institutions that have been working in isolation and are usually understaffed and under-resourced, to work toward a common set of goals, thereby achieving coordinated outputs that illustrate the high value and impact of their collections.

fungaria is very poorly documented at even high taxonomic levels making in-depth analysis of representation of these collections impossible. At a collection institution level, most preserved collections are found in Europe and North America. The analysis of GBIF data suggests that 90% of vascular plant species are represented in preserved collections, but only 55% of fungi species. Asia, northern and central Africa and Amazonia are relatively under-represented. Meyer et al. (2016) also noted a relative under representation of countries with emerging economies.

8.1.1 | Geographic and taxonomic gaps

Meyer et al. (2016) report that high geographic coverage of collections was often associated with the botanical interests of institutions and major research and data mobilization programmes. Collection and digitization programmes need to consider where they can have the most impact on research and conservation and in part will be driven by the policies of biodiverse countries. There is a tension between the general collection and digitization to fill geographic and taxonomic gaps and focused collection to provide evidence to solve particular science questions or societal challenges. Sampling of under-collected areas could be made more efficient by greater coordination of institutional priorities (Box 2). This coordination could be provided by existing regional initiatives such as the Latin American Botanical Network (http://www.rlbbotanica.org) or the Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale (http://www.aetfat.org/about/), the Distributed System of Systematic Collections (DiSSCo, http://dissco.eu) in Europe or international bodies such as the International Mycological Association (http://www.ima-mycology.org/).

Collection programmes should consider expanding their collections of fungi, bryophytes, and living material for botanic gardens and seed conservation facilitating a greater range of research and understanding of the diversity of the area. Living material not only supports conservation initiatives but also serves to engage a broader public in the research (Bakker et al., 2020). Collection of sterile

BOX 4 Developing fungal culture collections

More than 80% of the currently described fungi are not available as living samples for study. A coordinated approach is needed to address this enormous deficiency in availability of samples and data to support research and development. Scientific societies have developed to support the establishment and operation of microbial resource collections, at the national, for example, UK Biological Resource Centre Network, United States Culture Collection Network, at the regional level, for example, European Culture Collections' Organisation, and at the global level, for example, the World Federation for Culture Collections. However, networks with defined infrastructure and agreed strategy with the mandate to set coordinated strategy and work programmes are clearly required. The Organisation for Economic Cooperation and Development (OECD) recognized this situation and provided the framework for best practice and biological resource networking (OECD, 2001, 2007). It proposed a Global Biological Resource Centre Network (GBRCN) to integrate services and resources, encourage innovative solutions, provide coherence in the application of quality standards, allow homogeneity in data storage and management, and facilitate workload sharing. National and regional efforts have been initiated to establish the GBRCN with the aim to build a structured, long-lasting global network, enabling collections to meet user needs since the publishing of the report on these activities (Fritze, Martin, & Smith, 2010). Currently, GBRCN has advocates in North and South America, Africa, Asia and a strong base in Europe. The Microbial Resource Research Infrastructure (MIRRI, www.mirri.org/cgiar) is being established as a first step to creating the GBRCN.

material as vouchers derived from ecological studies in such areas can also shed light on true species diversity (Baker et al., 2017).

8.1.2 | Supporting collections-based science

Strengthening collections in tropical biodiverse countries and countries with emerging economies should be an international priority and financial mechanisms need to be developed to support the development of collections-based science (Heywood, 2017). Often funding is project based and focused on short-term delivery. It is crucial that long-term national infrastructure is developed which in turn can provide support to shorter-term projects. The creation and support of expertise in collecting, managing, and using collections is also important. For example, Ethiopian government support and Swedish aid funding enabled the development of the Ethiopian National Herbarium and training of Ethiopian nationals to create a centers of expertise for the country and the surrounding region (Demissew, 2014). Box 3 gives a further example of national level support and Box 4 focuses on fungi.

BOX 5 GBIF BID programmes

The GBIF Biodiversity Information for Development (BID, https://www.gbif.org/programmesme/82243/bid-biodiversity-information-for-development) programmes provide an example of building digital infrastructure. Funded by a grant from the EU Devco (EuropAid) and the Biodiversity Information Fund for Asia funded by the Japanese government, the programmes funded capacity enhancement and data mobilization into the GBIF network from sub Saharan Africa, the Caribbean, southeast Asia, and the Pacific Islands, all under-represented in GBIF. The impact of the BID over the first four funding calls has been substantial with 67 new data publishers mobilizing over 1.3 million new occurrences, including 39,000 taxonomic names of which nearly 2,400 were new to the GBIF network. In addition to mobilizing biodiversity data the BID programmes directly trained 120 people in data mobilization and use skills and that impact was multiplied to nearly 1,500 people through 66 replication workshops. The program shows the potential impact of targeted data mobilization to close data gaps and GBIF is pursuing additional funding to expand the projects.

8.2 | To what extent are data from biological collections digitally accessible?

8.2.1 | Digitization and data mobilization

Only 21% of preserved collections are available via GBIF, and 95% of these records cover only 38% and 26% of vascular plant and fungal species, respectively. Knowledge of the large proportion of collections which are not digitized could be improved by a standardized approach to gathering metadata about the collections, facilitating targeted digitization of non-digitized collections (Berendsohn & Seltmann, 2010; Owens & Johnson, 2019; GBIF recently ran a consultation, https://discourse.gbif.org/t/advancing-the-catalogue-of-the-worlds-natural-history-collections/1710). International initiatives such as the GBIF BID programme (Box 5) and the Global Plants Initiative (Ryan, 2013) have provided funding to accelerate digitization. The lag in data mobilization noted above limits available data and is a serious barrier to research. Meyer et al. (2016) note that locally available funding and participation in data sharing networks facilitate mobilization of data and Colli-Silva et al. (2020) provide a Brazilian example of this. Citizen science platforms such as iNaturalist (Heberling & Isaac, 2018) and the growth of observation data in GBIF demonstrate the potential for increasing the number of recorded occurrences and enable a broader audience to participate in annotating the specimen regarding its identity or other attributes of the organism, and enhancing or correcting the data provided with the original collection. Persistent identifiers on specimen data will enable the tracking of specimen use and citation measures. Unique identifiers are also critical for linking of specimen information to other genomic, trait or relationship data and for linking the occurrence of the specimen in different datasets or aggregators and ensuring information subsequently added to the specimen is available to all potential users (Bakker et al., 2020; Hedrick et al., 2019; Lendemer et al., 2020).

8.2.2 | Data quality

The inaccuracies in geographic coordinate information and inconsistency of use of taxonomic names on collection data create difficulties in analyzing data sets (Ball-Damerow et al., 2019; Meyer et al., 2016; Mounce et al., 2017). Paul and Fisher (2018) and Ball-Damerow et al. (2019) stress the importance of creating better automated solutions to flag errors, such as the newly developed software CoordinateCleaner (Zizka et al., 2019) and efficient mechanisms to report and correct data quality issues back to the source. Although automated flagging of erroneous records can improve certain analyses (e.g., Maldonado et al., 2015) it is often crucial that specialists validate results in a critical way in relation to their taxonomic group of expertise (Zizka, Carvalho, et al., 2020). Making linkages between preserved specimen duplicates will help propagate annotations made on one specimen to other duplicate specimens reducing curator time and increasing data quality (Nicolson, Paton, Phillips, & Tucker, 2018). Also, linking field images to specimen data via platforms such as iNaturalist will also assist broader, community level curation (Heberling & Isaac, 2018). The more complete the data associated with the specimen, the more potential uses it will likely have. A standard method for identifying the extent of digital information available from specimens in a collection is being developed (Wu et al., 2018).

Recognizing the need for greater alignment between biodiversity informatics related effort, GBIF hosted the second Global Biodiversity Informatics Conference in 2018. An outcome of the conference was a call for action (Hobern et al., 2019) that initiated the Alliance for Biodiversity Knowledge. The still developing alliance is providing a framework for collaboration with explicit goals of reducing duplication and providing global opportunities to be involved through virtual video workshops.

8.3 | What new collection types are needed to support research?

Traditional collection types are likely to remain central to future use, although collecting should be more routinely expanded to include ecological plot vouchers, biobank samples, and living material. In addition, new techniques and collection types will be necessary to support some lines of future research. Two such areas are new approaches to seed conservation and environmental sampling.

8.3.1 | New approaches to seed conservation

Several important megadiverse areas are currently under-represented in seed banks. For example, Teixido et al. (2017) and Silveira et al. (2018) highlight the relatively slow progress in banking the Brazilian flora. Among woody species of highly biodiverse tropical moist forest ecosystems, the proportion bearing desiccation-sensitive ("recalcitrant") seeds is estimated to rise to almost half, or possibly more (Wyse & Dickie, 2017). Together with the logistical difficulties of collecting seed samples from such vegetation, this significantly limits the role for ex situ seed preservation as a means of achieving conservation goals for these species, perhaps especially the most highly threatened ones (Wyse et al., 2018). Research is needed, both to further confirm the proportions and identities of recalcitrant species in various vegetation types; and, for high priority species, to develop alternative ex situ conservation methods, probably involving cryopreservation of excised embryos (Li & Pritchard, 2009).

Experience of conventional large-scale wild species seed banking has revealed considerable variation among both species and accessions in projected storage lives, such that the storage periods may not be sufficient to achieve conservation goals (Colville & Pritchard, 2019). Further research is needed to understand the basis of this variability, to be able to predict species likely to be short-lived in conventional storage; and to develop alternative storage protocols (e.g., cryopreservation in liquid nitrogen) to extend useful storage lives.

Where botanic gardens do exist in tropical regions they are often lacking in conservation capacity and suitable facilities for conserving tropical species in their countries of origin. International partnerships and collaboration are going some way to address this issue, for example the Meise Botanic Garden in Belgium is providing support for the development of coffee field gene banks in the Democratic Republic of Congo (Stoffelen et al., 2019). It is important that strong relationships with the users of collections are created to help demonstrate the value of the collections and the impact they can make on issues such as agricultural development and supporting the economy.

8.3.2 | Environmental sampling

The ability to isolate and sequence DNA from environmental samples (eDNA) such as soil, water, or plant material to study the plant microbiome has greatly enhanced our ability to identify organisms present in such samples. However, as techniques for eDNA studies develop, comparability for different studies using different techniques becomes difficult and this can be particularly problematic for monitoring studies (Jarman et al., 2018). Jarman et al. (2018) suggest that eDNA biobanking using standardized procedures would solve this problem allowing voucher material to be kept for reanalysis and comparison. The eDNA, the environmental sample, or both could be banked. Standards for storage and metadata are being developed by the GGBN (Droege et al., 2016).

8.4 | User engagement

Although much can be done with existing resources, engaging with a broad range of users will help recruit resources to assist with the development of collections to better address user needs. Kvaček *et al*. (2016) identify use cases of collections data in health, food security, sustainable agriculture and forestry, bioeconomy, climate change mitigation, management of raw materials, promoting innovation in society, and environmental security. Clearly, the potential use cases for collections are expanding into new areas (Bakker et al., 2020).

Recent work on coffee provides a compelling example that covers several use areas, demonstrating how collection data were used to help assess the risks and opportunities for wild and farmed coffee in Ethiopia, in the context of climate change and other conservation pressures and biodiversity loss (Davis et al., 2019; Davis, Wilkinson, Williams, Baena, & Moat, 2018; Moat et al., 2017). This work has been included in Ethiopian government policy and used by a broad range of stakeholders. The researchers estimate that if their work on building climate resilience in the coffee economy in Ethiopia is taken up, it would result in an increase in export revenue of at least US$3 billion over the next 20 years, based on achieving just 10% of the total potential identified (Hayter, Dobbs, & Gianfrancesco, 2019).

There is a risk that if collections are not used they can be lost. For example, the loss of culture collections can be inferred through the allocation of unique identifiers to registered collections in the World Data Center for Microorganisms. The database currently lists 791 culture collections, but this number has reached up to 1,230, suggesting that 439 collections have been lost or closed. Boundy-Mills et al. (2019) demonstrate that rescuing collections into proactive institutions can result in new uses such as studies of dyes and pigments and fungal infections of humans and animals. Chabbi and Loescher (2017) note that it is difficult for environmental research infrastructures to engage beyond their initial user base and that successful infrastructures rely on being used and on developing a sense of ownership with stakeholders. Collections infrastructures such as DiSSCo face a similar challenge. However, they can provide the overall coordination for a broader engagement with potential stakeholders than would be possible for a single institution.

9 | CONCLUSIONS—FUTURE LOOK

Data and material from collections can support a much broader range of study and use than has been seen historically and currently. Increase in use has been enabled by the development and wide accessibility of DNA sequencing technologies and other molecular analyses which expand the utility of collections (Bakker et al., 2020), the increase in computer power to analyze vast amounts of data, the development of web technologies allowing the semantic linking of information and the proactive engagement of potential users. The actions suggested below would help capitalize on these developments and maximize the impact of collection data on research and societal challenges:

- Governmental and international aid agencies should aim to support long-term collection facilities and staff training, including collecting from identified biodiversity hotspots and poorly explored areas. This infrastructure will better support short-term funded projects to develop societal benefits from plant and fungal diversity.
- Collection-holding institutions should speed up digitization of collections. This will require changes in work practices and additional resources. Making all data visible via aggregators such as GBIF will greatly facilitate use, research and community curation to improve quality.
- There should be greater alignment between biodiversity informatics initiatives and standards such as agreed species level consensus taxonomies and use of specimen persistent identifiers. GBIF and the Alliance for Biodiversity Knowledge are playing a key role.
- Greater institutional coordination is needed to assist with both in-depth collection of a broad range of taxa in key areas to address national priorities and also targeted collecting in under-collected areas. Regional and international initiatives that bring botanists and mycologists together could better coordinate activity to fill gaps.
- Institutions should invest in environmental biobank collections, following and developing GGBN data standards to better represent fungal material.
- Further research into the low-temperature ex situ storage of species with desiccation-sensitive seed is required.
- Collections-based institutions should work together to proactively build relationships with their current and potential new users.

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AUTHOR CONTRIBUTIONS

A.P. and J.D. devised the paper, and wrote and edited the manuscript. M.J., U.L., J.Moat, N.N., M.R., S.S., D.S., B.T., and T.W. analyzed data and wrote and commented on the paper. A.A., M.C., R.C.F., N.D., S.D., G.D., T.F., A.G., N.H., J.Miller, and J.V. wrote and commented on the paper.

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