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Review

Fungal biodiversity and conservation mycology in light of new technology, big data, and changing attitudes

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SUMMARY

Fungi have successfully established themselves across seemingly every possible niche, substrate, and biome. They are fundamental to biogeochemical cycling, interspecies interactions, food production, and drug bioprocessing, as well as playing less heroic roles as difficult to treat human infections and devastating plant pathogens. Despite community efforts to estimate and catalog fungal diversity, we have only named and described a minute fraction of the fungal world. The identification, characterization, and conservation of fungal diversity is paramount to preserving fungal bioresources, and to understanding and predicting ecosystem cycling and the evolution and epidemiology of fungal disease. Although species and ecosystem conservation are necessarily the foundation of preserving this diversity, there is value in expanding our definition of conservation to include the protection of biological collections, ecological metadata, genetic and genomic data, and the methods and code used for our analyses. These definitions of conservation are interdependent. For example, we need metadata on host specificity and biogeography to understand rarity and set priorities for conservation. To aid in these efforts, we need to draw expertise from diverse fields to tie traditional taxonomic knowledge to data obtained from modern -omics-based approaches, and support the advancement of diverse research perspectives. We also need new tools, including an updated framework for describing and tracking species known only from DNA, and the continued integration of functional predictions to link genetic diversity to functional and ecological diversity. Here, we review the state of fungal diversity research as shaped by recent technological advancements, and how changing viewpoints in taxonomy, -omics, and systematics can be integrated to advance mycological research and preserve fungal biodiversity.

Introduction

The methods used to quantify fungal diversity have changed drastically over recent decades. An enormous body of knowledge has been amassed through the construction and refinement of intricate taxonomic keys dedicated to distinguishing fungi based primarily on morphology. However, the advent of high-throughput sequencing, along with shotgun and targeted metagenomics, has demonstrated the existence of vast pools of previously undetected biodiversity. It is now recognized that many fungi lack the distinguishing morphological characters necessary to delineate species based on morphology alone[1,2], making holistic approaches that incorporate diverse data such as biogeography, ecology, chemotyping, population genetics, phylogenetics, and genomics essential for characterizing fungal biodiversity[3–5]. In 2018, DNA sequence analysis was used in 94% of published fungal taxonomic studies[6]. Estimates of the total number of fungal species in existence have varied widely with the incorporation of new, and often increasingly complex, models. Hawksworth updated his original estimate of 1.5 million species, approximated using plant:fungal ratios from well-studied habitats[7], to 2.2–3.8 million by weighting those ratios by geographic distribution, known genetic richness, and lifestyle[8]. Less conservative figures range from the often-cited number of 3.5–5.1 million species estimated using DNA markers amplified from soil and extrapolated to plant:fungal ratios[9], to 6.3 million extrapolating from high-throughput sequencing data[10], and up to 11.7–13.2 million species based on meta-analysis of taxa recovery by culture-dependent versus culture-independent methods[11]. In all of these cases, the estimates of total fungal species diversity swamp the mere 146,155 species currently described (https://www.catalogueoflife.org/annual-checklist), which account for only 1.2–14.6% of the total potential species pool. The number of new species descriptions added per year currently averages around 2,000 — an increase over the last decade that shows no sign of saturation, and which is thought to be driven in large part by molecular methods for species delineation, reclassification and taxon splitting[12,13]. Despite this increase, at the current rate of description, it will take generations of work before we have named and described enough species to adequately assess the true diversity of the fungal kingdom.

Sources of newly appreciated fungal diversity

Enabled in large part by advances in molecular genetics, investigations of cryptic environments and novel substrates have

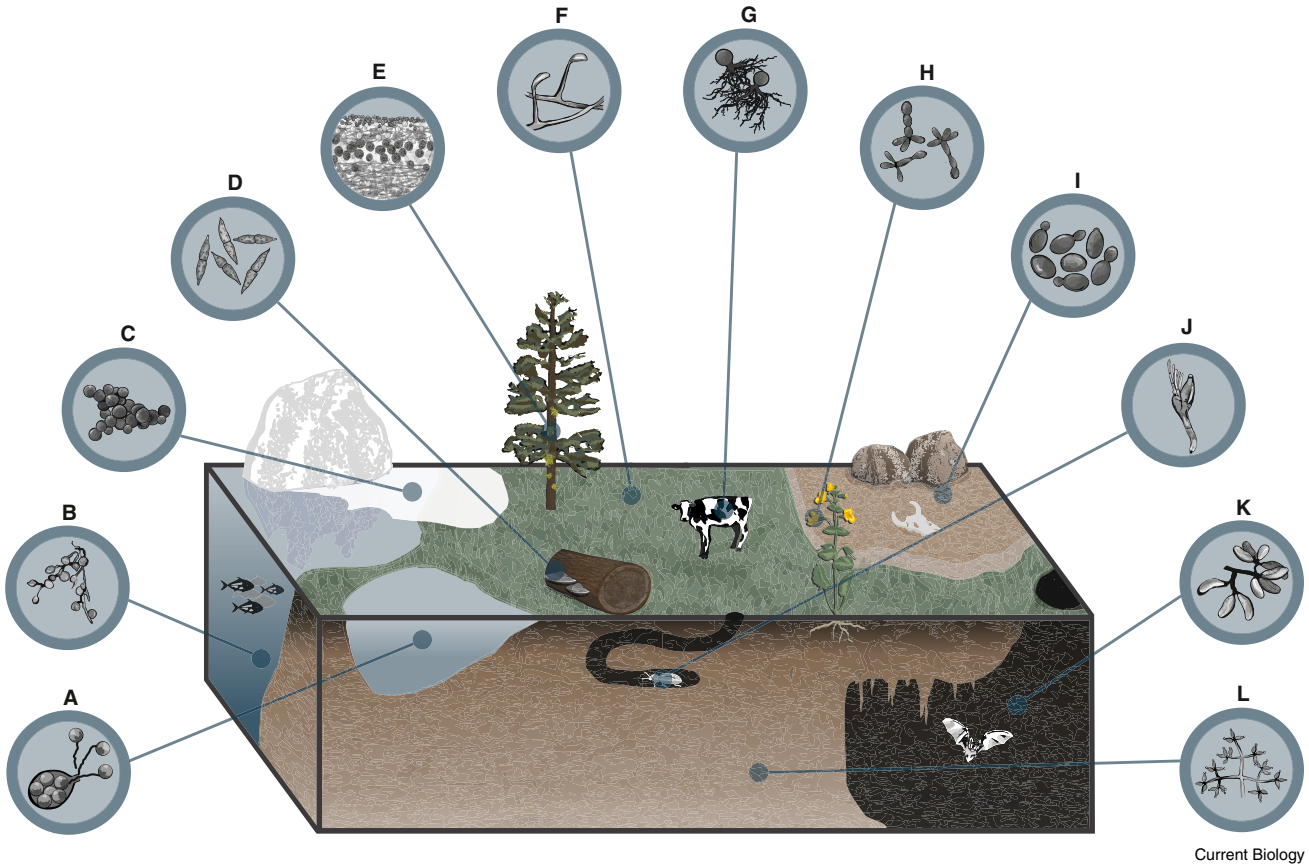

Figure 1. The discovery of fungal diversity from previously underappreciated habitats.
Although representatives from each system are depicted as sporulating, many of the fungi being discovered in these systems lack phenotypically diagnostic features such as obvious sporulation, making molecular technologies critical to their discovery and characterization. Representatives depicted in icons are listed in parentheses. (A) Fresh water (*Batrachochytrium* sp.). (B) Marine habitats (*Posidoniomyces atricolor*). (C) Arctic and glacier systems (*Cryptococcus* sp.). (D) Fungicolous fungi associated with other fungi (*Hypomyces* sp.). (E) Lichens (*Letharia vulpina* with *Tremella* sp. and *Cyphobasidium* sp.). (F) Endophytes of plant roots, shoots, and leaves (*Epichloë* sp.). (G) Anaerobic gut fungi (*Neocallimastix*). (H) Nectar yeasts (*Metschnikowia gruessii*). (I) Endoliths living in and on rocks, and desert fungi in association with bio crusts (*Bacillicladium* sp., yeast form). (J) Arthropod-associated fungi (*Laboulbenia pedicellate*). (K) Cave- and mine-associated fungi (*Pseudogymnoascus* sp.). (L) Soil-associated fungi (*Trichoderma harzianum*).

highlighted the magnificent breadth of niches occupied by fungi. In recent years, these studies have yielded previously unknown fungal diversity in lichens[14,15], rock[16], glaciers[17], marine and fresh water systems[18–23], caves[24], floral nectaries[25], inside foliar and other plant tissues[26] and in association with other fungi[27] (Figure 1). Marine systems make an excellent case study of this newly appreciated diversity; fungi were once considered a rare component of marine environments, but culture-independent methods revealed their widespread distribution and diversity in marine systems. Currently more than 1,100 species of marine fungi have been described[20], a number that likely represents only a small percentage of the total species pool, as many more are detected but unknown to science[28]. These species are phylogenetically diverse, representing both known groups and undescribed deep-branching lineages, and demonstrate morphological and functional diversity, niche differentiation, and biogeographic stratification (see Vargas-Gastélum and Riquelme[29] for a recent review). Marine sediments are estimated to harbor a proportion of fungal biomass equivalent to terrestrial soil, although these estimates often include both active community members and inactive DNA of both marine and terrestrial origin[30]. Like with investigations into terrestrial fungal systems, the push to incorporate metabolomics and proteomics approaches will help illuminate the proportions and identities of the active components of these marine communities, and help to characterize fungal metabolites that can be applied for clinical and biotechnological use[29,31].

Although fungi colonize nearly every environment on earth, fungal diversity is not uniformly distributed. Fungi display high levels of endemism, and environmental filtering mediates the differential abundance of taxa and functional groups via complex interactions between biotic and abiotic factors, such as the co-localization of fungal host species, temperature, moisture, altitude, pH, and nutrient availability[32–35]. For example, although fungal endophytes, saprotrophs, and parasites display a typical latitudinal diversity gradient, the diversity of ectomycorrhizal fungi tracks the diversity of their host trees, putatively displaying the highest richness in temperate zones[36,37]. Likewise, whereas the abundance and diversity of ecto- and arbuscular mycorrhizal fungi generally decline with increasing nitrogen availability,

saprotrophs and plant pathogens often display the opposite pattern[38–42].

Changing attitudes toward categorization

Because of their immense impact on human systems, fungi have been traditionally characterized by the outcomes of their interactions with animals and agriculturally important crop species: that is to say, species X is a 'pathogen' because important crop Y dies when infected by X. However, there is mounting appreciation for both functional guild fluidity and the importance of interspecific variation. It is clear that many fungal species classically assigned to a single guild take on the roles of other guilds at different life stages, when in association with different host species, or when exposed to different environmental variables. Examples include *Botrytis* species, which can act as either endophytes or pathogens depending on the life stage of the host[43], and *Fusarium graminearum*, which can act as an endophyte or a pathogen depending on host species[44]. Similarly, there is considerable variability in nutrient exchange between arbuscular mycorrhizal fungi and host depending on host life stage, environmental factors, and fungal intraspecific variation[45,46]. Metagenomics and pan-genomics have facilitated recent revelations regarding diversity within a species, both helping to define fungal individuals and highlighting the importance and magnitude of intraspecific genetic differences[47,48]. These techniques have shown that in addition to gene variants (insertions, deletions, and single nucleotide polymorphisms), a single species can contain significant variation in the presence/absence, copy number, and structural arrangement of both genes and chromosomes. There is a growing appreciation that assessment methods are key to detecting this variation; for example, fungi are commonly grouped by DNA sequence similarity into 'operational taxonomic units' by clustering marker regions at 97% similarity. This cutoff is intended to approximate species-level differentiation while accounting for variation and sequencing errors. However, recent work has shown that subtle patterns of intraspecific diversity can be missed at this cutoff, and some investigators now advocate for the use of 'amplicon sequence variants' over operational taxonomic units, as the former recognizes single nucleotide changes between sequences[49]. The recognition of intraspecific diversity has been further facilitated by the adoption of techniques for constructing *de novo* assemblies that are not constrained by the gene repertoire of reference genomes, and novel techniques that negate the need to obtain axenic cultures prior to sequencing[50,51]. These technologies have been particularly important for investigating fungi that inhabit extreme, cryptic, or difficult-to-access environments. For example, single-cell sequencing has enabled investigation of fungi from environments that are difficult to analyze using traditional means — such as the targeting of single nuclei within the multinucleated spores of arbuscular mycorrhizal fungi[52] — and has facilitated the phylogenomic placement of unculturable, early-diverging species in the Cryptomycota, Chytridiomycota and Zoopagomycota[53].

The challenge and opportunity of environmental sequence data

The accessibility and widespread adoption of high-throughput sequencing, particularly the sequencing of fungal markers such as the 'internal transcribed spacer' region (ITS; designated as the universal barcode region for fungi), has greatly accelerated our understanding of fungal diversity, function, and biogeography[10,37,54]. These techniques span a diversity of protocols, sequencing platforms, and analysis pipelines (see Nilsson *et al.*[55] for a recent review) with ever increasing affordability, and have driven the democratization of DNA sequence analysis and the investigation of complex microbial communities. However, high-throughput sequencing is not without challenges, including a risk of decoupling organismal expertise from fungal community analysis and the fact that many sequences generated during high-throughput sequencing analyses cannot be taxonomically assigned to species.

The increased accessibility of high-throughput sequencing has enabled researchers to investigate fungal communities without the requirement of mycological training. This has raised concerns about the potential for increased bias in the ecological and functional interpretations based on these results[56]. Despite worries that the -omics revolution would bring about a generation of computational specialists who are detached from the biological systems that they study, organisms remain at the center of mycological research. Although specialization has increased, so has cross-discipline collaboration. High-throughput sequencing in particular has been responsible for bringing outside specialists into the mycological fold, facilitating the graceful incorporation of fungi into fields traditionally designed around bacterial targets, such as the human microbiome[57], clinical diagnostics[58], and the rumen of herbivorous mammals[59].

Given the small number of accepted species relative to the total estimated fungal diversity, the fact that many of the sequences generated during high-throughput sequencing analyses cannot be taxonomically assigned to species (or at times to genus or higher classifications) is not surprising. Importantly, a lack of barcode sequence homology does not imply that a sequence belongs to an undescribed species, as the barcodes of many described species have yet to be added to digital repositories[60]. It is unknown how many currently unmatched sequences could be assigned if type material for all named species were represented in sequence databases. However, given the 16 billion fungal ITS reads currently housed in NCBI's short read archive[61], it is likely that vast pools of unmatched sequence reads representing novel taxa would remain.

Currently, the international code of nomenclature for algae, fungi, and plants (*The Code*) does not accept DNA as a type, preventing the formal description of taxa known only from sequences. The problem of how to address the naming of these taxa is one of the most significant and controversial issues currently facing mycology (see Zamora *et al.*[62] and Thines *et al.*[63] for recent discussions). The issue has spurred heated debate, and many solutions have been proposed[64,65], including amendments to *The Code* and functional workarounds such as the use of persistent alphanumeric identifiers (like those employed by the UNITE database (https://unite.ut.ee) (Figure 2). Arguments against the use of DNA as a type include concerns over data quality control, the number and identity of DNA regions needed to make a taxonomic determination and prevent taxonomic instability, how to prevent the creation of redundant or artificial names, and the charge that the absence of type

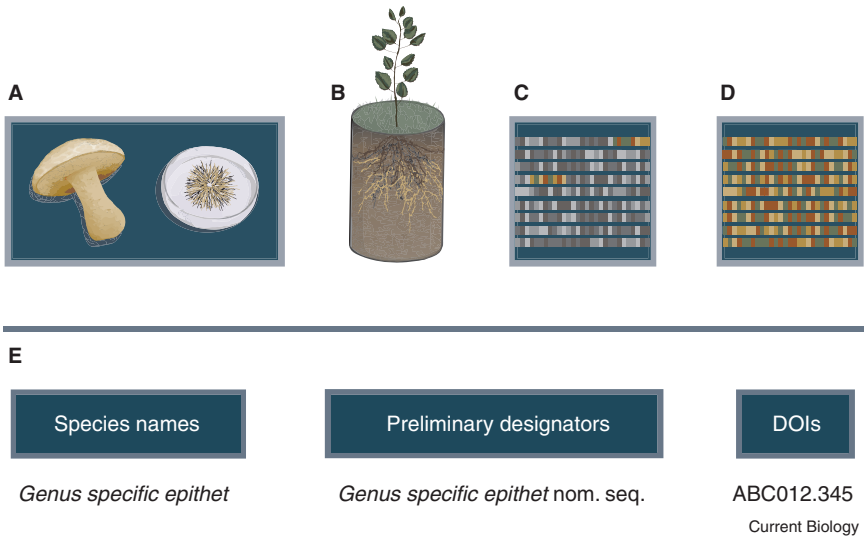

Figure 2. What should constitute a 'type'?
(A) Vouchers are typically preserved specimens deposited in permanent, accessible facilities such as herbaria and fungaria. Type material for fungal species descriptions typically takes the form of vouchered fruitbodies or preserved cultures (or an image in rare cases). However, many fungal taxa are known only from DNA and cannot be described via the current requirements of the International Code of Nomenclature for algae, fungi, and plants, and the suitability of alternative type material is hotly debated. Proposed alternative forms of type material include (B) substrates from which the high-throughput sequencing data were generated (mixed consortia known as 'bag-types'), (C) DNA barcodes or longer sequence fragments such as whole rDNA cistrons, or (D) whole genome sequences. (E) Alternatives to amending the current standards for species descriptions include the assignment of provisional names, or persistent alphanumeric identifiers.

material will prohibit the collection of additional data, reassessment, and verification using more traditional taxonomic approaches[62,63].

As sequencing technologies rapidly progress, the generation of whole closed fungal genomes from environmental samples may soon be within reach for fungi as it is now for bacteria[66], addressing at least some of the concerns related to using DNA for fungal type material. Long-read sequencing of the full ribosomal RNA-encoding (rDNA) cistron may offer a middle ground and provide a viable alternative for resolving phylogenetic relationships of some difficult taxa using a single region[67]. Although *The Code* officially allows for types in the form of mixed samples, the use of substrate submissions for cryptic taxa (the substrate sequenced to produce unmatched high-throughput-sequencing reads) is discouraged[61]. Regardless of the viability of assigning these mixed samples as type material in the future, preservation of substrates used for high-throughput sequencing is a valuable investment. Although it should be noted that substrate preservation is not always possible (destructive sampling is sometimes required), preserving these resources would enable future analyses as advances in microfluidics, single-cell sequencing, and in-situ visualization techniques continue to improve[68]. However, this would require the development and standardization of methods for preservation of diverse complexes of materials (such as soil, fecal matter, and rumen). Initiatives such as the Earth BioGenome Project and the Global Genome Biodiversity Project are working to preserve and standardize access to DNA and high-quality tissue samples but focus mostly on animals and plants[69–71]. Ultimately, increasing the chance that a sequence database search will match a named species will entail continuing efforts to populate databases by sequencing existing type material (including surmounting the challenges associated with sequencing very old specimens of variable preservation quality[60,72]). Success will also depend on increasing the number of described fungal species (with appropriate cataloguing of their associated barcodes) and community consensus on how to assign names to the numerous taxa known only from sequence data.

Linking functional diversity to taxonomic diversity

One of the most significant challenges facing mycological research is to couple genetic diversity to functional diversity. Genome sequencing has opened up new avenues for the prediction of gene function, clarified the phylogenetic history of important proteins, domains, and gene families, and facilitated functional mapping of active transcriptional responses to a plethora of environmental stimuli. Databases cataloging fungal functional activities, including the integrated progression of FunGuild[73], Fun^{Fun}[74], and FungalTraits[75], have enabled researchers to make functional predictions from mixed environmental samples. However, functional predictions will remain putative until they can be validated in the context of living organisms, making culture-dependent research, and the improvement of fungal culture techniques, central to research progress. Among new technologies, advances in molecular genetics, metabolomics, microfluidics, imaging, chemical ecology, and nutrient tagging are generating excitement and valuable insights into fungal function.

Molecular genetic techniques for elucidating fungal functional diversity at the level of individual genes have long been staples in mycological research but remain nascent for non-model fungi. The advancement of novel genetic transformation systems, such as the recently developed system for the chytrid *Spizellomyces*[76], promises to open doors to confirm the function of genes in diverse fungal groups. The further development of genetic manipulations — including transformation and CRISPR–Cas9-directed mutagenesis (particularly, surmounting the technical hurdles to transforming fungal dikaryons) — will enable research that has until now been out of reach for mycologists working outside of model systems.

Advances in metabolomics and chemical ecology have proven particularly important in lichens, where metabolic profiling is used for taxonomy[77,78], and for identifying chemical exchange during interkingdom interactions. These interactions include the complex crosstalk that occurs during the process of fungal pathogen infection[79] as well as between mutualistic fungal endophytes and their host plants[80]. Uehling *et al.*[81] demonstrated the

power of combined approaches for elucidating interspecies interactions using a metabolomics–microfluidics system to describe the relationship between *Mortierella elongata* and growth-promoting *Burkholderia* bacteria. Microfluidics are emerging as a novel technique to investigate fungal functional and trait diversity in real time; recent examples include insights into the dynamics of fungal endosome trafficking[82], tradeoffs between fungal traits such as growth rate and cell plasticity[83], and how diverse fungi search and navigate complex microenvironments[84,85]. Advances in single-cell imaging promise to further increase the resolution of fungi within these microenvironments, as exemplified by the recent application of infrared spectroscopy to *in situ* chemical imaging of the decomposition activity of individual hyphal tips in the ectomycorrhizal species *Paxillus involutus*[86]. New applications to older imaging technologies also continue to aid in resolving fungal structure, including visualizing the distribution of third-party basidiomycete yeasts in lichen thali using fluorescent *in situ* hybridization[15], and fluorescent protein-tagging to characterize 'toxisomes' — unique trichothecene biosynthetic and transport complexes formed in *Fusarium graminearum*[87]. Finally, advances in nutrient tagging and tracking are enabling researchers to investigate resource exchange between individuals at unprecedented scales, such as the investigation into partner choice and nutrient sanctioning using quantum-dot fluorescent nanoparticles to track the exchange of nitrogen[88] and phosphorus[89] in arbuscular mycorrhizal fungi. Likewise, the development of stable isotope probing, when coupled to high-throughput sequencing, has allowed researchers to link fungal community members with specific nutrient dynamics, such as taxon-specific rates of fungal cellulose degradation[90] and temporally variable carbon dynamics in grasslands[91]. Lastly, nano-secondary ion mass spectrometry has identified fungal spores as potential regulators of sodium salt dynamics and cloud formation[92].

A role for community science in fungal diversity research

Public engagement is critical to conservation efforts and has immense potential to aid in the mapping and characterization of as-yet undescribed fungal diversity. Historically, contributions to fungarium collections from the public, amateur societies, and other non-academic sources have been key to both amassing fungal collections and the identification and characterization of fungal species[93,94]. Today, platforms such as iNaturalist (http://www.inaturalist.org) and Mushroom Observer (https://mushroomobserver.org/) have created both new avenues for engagement between professional mycologists and community scientists, as well as powerful tools to locate rare species and, more generally, document geographic distribution, phenology, and frequency. The data aggregated by these platforms are invaluable for conservation efforts; for example, the International Union for Conservation of Nature working group, Macrofungi of North America, relies heavily on data from community science platforms to construct risk assessments and nominate species for Red List status. Like fungarium collections, these platforms are prone to sampling bias that privileges charismatic macrofungi and geographic regions where participants live[95] (Figure 2). Geotagged observations vary in both the quality and quantity of their associated metadata but are bolstered by community curation that validates proposed species identifications. In addition to encouraging more taxonomic experts to aid in validating community science records, crowdsourced data can be further improved by supporting training initiatives for community scientists, such as those administered by the Fungal Diversity Survey (https://fundis.org) and the Continental Mycoblitz (2019) (https://www.inaturalist.org/projects/continental-mycoblitz-2019). Increasing awareness of best practices for logging observations — including how to photograph and preserve specimens, and how to identify and log important traits, ecological notes, and other metadata — will increase both data quality and community knowledge.

Targeted community science initiatives have also been successfully undertaken; for example, the Danish Fungal Atlas project has amassed over 235,000 community science contributions of Basidiomycota, including 197 species new to Denmark and at least 15 species new to science, and has moreover documented species declines associated with soil acidification and nitrogen deposition[96]. Overall, community science platforms are helping to raise public awareness and appreciation of fungi and fungal diversity, and drive increases in the number of geotagged fungal observations, which inform more complete and higher resolution models of the distribution of rare species[97]. The spatial and temporal coverage of these types of crowdsourced data facilitate investigation of topics such as phenology and biogeography that would otherwise be difficult or impossible to address.

Conservation mycology

Although notably absent from historical conservation efforts, the protection of fungi and the development of conservation mycology as a subfield have grown considerably over the last decade[98]. It's clear that fungi are susceptible to the same anthropogenic factors that contribute to species decline in other organisms and, at the current rate of description, many species of fungi will risk extinction before they can be described and protected[99,100]. Heilmann-Clausen *et al.*[101] made one of the first formal arguments for fungal conservation by characterizing fungi as ecosystem hubs, bioindicators, providers of food, medicine, and biotechnology, and as a Rosetta stone for conserving other highly speciose organisms. Since then, the number of fungal species listed in the International Union for Conservation of Nature Red List has grown from 32 to 425 (https://www.iucnredlist.org/), a number that is still insignificant compared to the number of listed plants (50,369) and animals (78,126). Explanations for the neglect of fungi in traditional conservation efforts are many: these include stigma around protecting a group that is perceived as unglamorous and at times dangerous[98], assumed functional redundancy and a lack of functional characterization[101], and the technical difficulty of assigning species, defining populations, and assessing global distributions[102,103]. Assessing rarity is often the first step for conservation initiatives, but counting fungi is not as easy as counting other types of organisms; fruitbody counts are not only conditioned on seasonality and the ability to produce sporocarps in the first place, but have long been known to correspond poorly with other metrics of fungal abundance such as ectomycorrhizal root-tip counts[104] and the abundance of high-throughput sequencing reads[105]. Ectomycorrhizal root-tip abundance, in turn, also corresponds poorly

with soil mycelial abundance[106]. Conversely, gene copy numbers of ITS are extremely low in some taxa, such as *Microsporidia*[107] and *Pneumocystis*[108], and can be highly variable within taxa, including between individuals within the same population[109]. Additionally, some fungal groups display sequence variation between rDNA copies[110], impeding amplification and further complicating the reliability of high-throughput-sequencing barcoding for relative abundance assessments. Regardless of which tool is used for estimating fungal abundance, the process is innately coupled to theoretical issues concerning what constitutes a fungal individual in the first place, where a distinct entity can represent a single cell, or some of the largest organisms on earth[111].

New technologies and tactics are in development to remedy many of these issues. Spike-in internal DNA standards for fungal community analysis ameliorate some of the issues associated with abundance estimates from high-throughput sequencing[112,113]. Advances in metatranscriptomics coupled with improved databases of fungal functional activities have the potential to link genetic diversity to functional diversity[75,114], and metagenomic and amplicon studies (such as those now compiled in the GlobalFungi database) will aid in assessing biogeographic frequency[115]. Modeling efforts are underway to predict global fungal biogeography both now and under future climate regimes[116]. Efforts to link community science observations with diverse metadata (for example, the ClimFun database linking fungal phenology and climate change data) will help contextualize fungi in broader conservation and risk assessment frameworks[117]. These efforts will help set conservation priorities, but of themselves do not address issues relating to our inability to protect the vast biodiversity of fungal species.

Broadening the criteria for acceptable type specimens has the potential to increase the number of described species and, consequently, the number of species that can be protected using traditional conservation measures. However, traditional approaches may not be the most efficient or effective tactic for fungal conservation, regardless of the number of species targeted for protection[97]. Fungi are highly interconnected organisms, frequently engaged in (often obligate) associations with a multitude of interaction partners including plants, insects, vertebrates, protists, bacteria, and viruses. Because of this, fungal conservation is innately linked to the conservation of these fungal associates. Protecting consortia at the ecosystem level may effectively bypass the need to list individual fungal species and facilitate conservation without depending on defining individual species relative to traditional conservation value assessments, which are often unfeasible for cryptic and undescribed organisms[118]. In contrast to species-centric approaches that focus on assessing population declines, function, and habitat requirements for single species, ecosystem-level protections allow for prioritization schemes structured around broader metrics such as system connectivity or the identification of biodiversity hot-spots (including the potential to incorporate sequence-based community analysis that includes undescribed taxa). Additionally, the benefits of ecosystem-level protections extend well past the fungal kingdom[98]. Fungi are routinely used in restoration efforts[119] and form critical associations with rare or Red-Listed species across wetlands[120], aquatic environments[121], forests[122] and grasslands[123]. Because of the combination of high levels of connectivity, high diversity, and poorly characterized function, ecosystem-level approaches may be a more efficient tool for fungal conservation[101]. However, it has been noted that species- and ecosystem-level approaches are not mutually exclusive, and that adapting tactics to individual use may ultimately prove the most effective means for fungal conservation[124].

Expanding our definition of conservation to include diverse data

Just as type specimens enable reanalysis of raw data for future researchers, the preservation of raw -omics data, metadata, and code enables reproducibility and reanalysis. There is a growing emphasis on the importance of data protection, curation, and accessibility, typified by the priorities outlined in the FAIR principles[125] (https://www.go-fair.org/fair-principles), which state that data should be findable, accessible, interoperable, and reusable. Most journals now require the preservation of raw data prior to publication; the use of repositories such as NCBI's short-read archive (https://www.ncbi.nlm.nih.gov/sra) for raw sequence data, or treeBASE for phylogenetic data (https://treebase.org), Data Dryad for diverse raw datasets (https://datadryad.org), and protocols.io for wet-bench protocols (https://www.protocols.io) has become standard. Equally important is the increased usage of code archiving via repositories such as Zenodo (https://zenodo.org) and Figshare (https://figshare.com). Code archiving, along with clearly embedded annotations and versioning, is critical for enabling reproducibility and critical assessment of published methods and conclusions. However, far fewer journals require preservation of code than raw data, and there is still a disheartening frequency of publications with bioinformatic methods sections that simply state that a 'custom script' was used, preventing others from fully understanding, or building on the work presented. This is the wet-bench equivalent of stating that 'molecular methods' were used without further explanation. According to our informal poll, the slow adoption of stable code repositories in mycology stems from multiple concerns and misunderstandings within the community. These include a lack of confidence in the code itself (fears over publishing code errors, or publishing code that will be judged as 'inefficient' or 'ugly'), opinions around resource ownership and the right to code sequestration, and lack of training on how to annotate, version, and publish code in the first place. Similarly, disparities in the quantity and quality of associated metadata in repositories such as NCBI routinely result in incomplete datasets that are likely to limit secondary usage[126], including their utility in conservation assessments. Standardized repositories built around FAIR principles, such as GEOME[127] for sequence and ecological data, increasing education and community awareness around data preservation, and addressing the concerns to make code and data openly available in publications as noted above should be a priority for the mycology community and scientists more generally. The conservation of diverse data ensures reproducibility and enables more effective biological conservation by allowing information to be readily exchanged between diverse mycological subfields and the broader conservation community.

Table 1. A non-exhaustive list of notable fungal culture collections.

Culture collection and country	Size and focus of collection
American Type Culture Collection (ATCC) – United States	>79,000 fungal strains including >4,800 type cultures
Fungal Genetics Stock Center (FGSC) – United States	>75,000 fungal strains including many mutant libraries
BIOTEC (BCC) – Thailand	>60,000 fungal strains with a focus on entomopathogenic fungi
Agricultural Research Service Culture Collection (NRRL) – United States	>68,000 fungal strains with a focus on plant pathogens
CBS-KNAW culture collection – The Netherlands	>57,000 fungal strains
CABI Living Resource Collection – United States	>28,000 strains with a focus on agriculturally relevant fungi
Canadian Collection of Fungal Cultures (DAOMC/CCFC) – Canada	>20,000 fungal strains with a focus on plant pathogens and mycotoxigenic fungi
China General Microbiological Culture Collection Center (CGMCC) – China	>20,000 fungal strains
Genebank Project (NARO) – Japan	>17,000 fungal strains
BCCM/IHEM Fungi Collection – Belgium	>15,000 fungal strains with a focus on animal pathogens and allergenic fungi
Reference Culture Collection at the Center for Forest Mycology – United States	>12,000 strains with a focus on wood associated Basidiomycetes
The UAMH Center for Global Microfungal Biodiversity – Canada	>10,000 fungal strains with a focus on biomedically relevant fungi
Phaff Yeast Culture Collection – United States	>7,500 strains of yeast, including >1,000 different species and >200 novel species
Mycobase of the Muséum National d'Histoire Naturelle – France	>6,000 strains with a focus on saprophytic Ascomycetes and Zygomycetes
International Culture Collection of Vesicular Arbuscular Mycorrhizae (INVAM) – United States	>900 strains of arbuscular mycorrhizal fungi

The role of collections in securing diverse data

Herbaria, fungaria, and collections-based institutions house type specimens upon which species definitions are based, and they voucher the products of biodiversity surveys and scientific studies for preservation and reuse. These institutions are critical to cataloguing fungal diversity, generating knowledge, and mapping the abundance and distribution of fungi over time[128]. Collections ensure that specimens and specimen-derived data can be reevaluated in the future, as theory and technology advance. Collections offer a unique opportunity to assess rarity and extinction risk[129] and act as a direct window into the past, enabling the tracking of critical indicators of global change[130,131], pollution[132], epidemiology[133], biogeography[134], and evolution[135]. In recent years, there have been significant efforts to digitize collections, including searchable relational databases of photographs, metadata, and DNA. A prime example is MyCoPortal (https://mycoportal.org) — a database of collections spanning multiple universities, botanic gardens, museums, and government agencies that houses 7,394,281 occurrence records as of this writing. These entries have made many historic collections publicly accessible and have enabled new opportunities for machine learning and meta-analysis[136,137]. Despite these contributions, herbaria are currently under threat. The reprioritization of funding away from natural history-based research has resulted in the downsizing, closure, or relocation of many collections to larger centralized facilities[128].

Culture collections are another important axis to cataloguing, preserving, and making fungal diversity accessible to the research community. Fungal culture collections represent both large, long-standing repositories as well as numerous smaller stocks housed in private collections and herbaria[138,139] (Table 1). These collections vary in both size and quality, with the designation of 'microbial biological resource center' (mBRC) reserved for collections that adopt the standards set by the Organization for Economic Cooperation and Development or the International Organization for Standardization (ISO) standards for biobanks, entailing outside certification, tracking, and validation of strain identity and provenance[140,141]. Culture collections are particularly well developed for ascomycete yeasts, reflecting their importance to food production and biotechnology, and have been aided by the relative ease of preservation compared to many filamentous species[138,141]. Indeed, the ease and ability to preserve fungal cultures is highly variable; fungi that sporulate in culture have greater storage viability than vegetative cultures, whereas obligate symbionts are often maintained in labor-intensive co-culture[141]. Public access to published strains is essential for reproducibility and building on current research, but the deposition of strains into professional repositories remains low[142]. The U.S. Culture Collection Network, which is supported by the National Science Foundation's Research Coordination Network, aims to increase awareness of the benefits of culture repositories, coordinate best practices, and protect endangered collections, including fungi[140]. Currently, only ~17% of described fungal species are preserved in culture collections; these represent a sample that is heavily biased both taxonomically and geographically with the majority of cultures originating from Europe, North America and Asia[137] (Figure 3). Advances in our ability to culture taxa previously thought to be unculturable offer hope that we may be able to generate type material for many previously uncharacterized taxa[143,144]. However, it is likely that many species of fungi will remain difficult or impossible to isolate or maintain as axenic cultures due to phenomena such

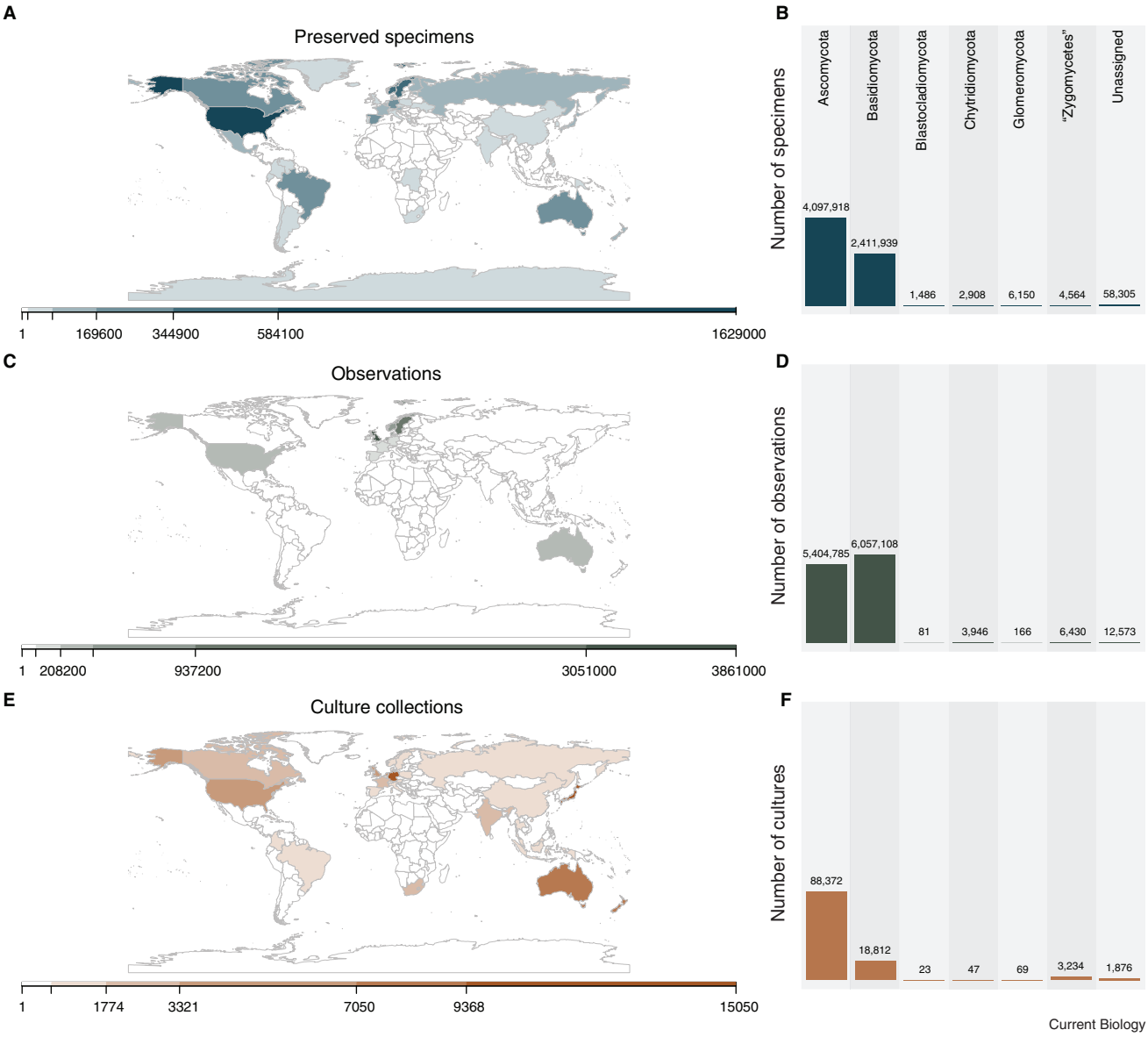

Figure 3. The global origin of fungal resources by phylum and resource type.
(A,B) Preserved specimens (such as those held in herbaria) display bias toward Ascomycota and collections from the US, Europe, and Australia. (C,D) Observations such as those made on community science platforms like iNaturalist are biased toward Basidiomycota, with participation concentrated in Europe, the US, and Australia. (E,F) Culture collections are greatly biased toward Ascomycota, reflecting their importance in industry and agriculture, with most collections isolated from Europe, Japan, Australia, New Zealand, and the US. Color gradient on (A,C,E) represents count data for each country. Data represent 6,583,270 records of preserved specimens from 249 countries, 11,485,089 observations from 202 countries, and 112,433 living cultures isolated from 205 countries. Data were downloaded from GBIF.org (27 April 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.9733fq. Maps and figure generated in the R programing environment, using ggplot2 and rworldmap. Scripts available at github.com/MycoPunk/CB_review (https://doi.org/10.5281/zenodo.4738456).

as obligate interspecies interactions, or metabolic syntrophy[145,146]. Cryopreservation facilitates the safeguarding of viable genetic diversity before extinction and may be particularly important for groups that cannot currently be cultured. However, most collections only accept isolated individuals, and many unculturable species cannot be separated from their microbial consortia or complex substrates[147]. In order for cryopreservation to be used to its full potential, curators and funding bodies must see the value of accepting mixed samples, coupled to investment in improved methods for the storage of microbial consortia[148].

The conservation of knowledge and the interdependence of classic mycology and modern approaches

Fungi are extraordinarily connected organisms, forming complex interaction networks at multiple ecological scales. Just as conservation efforts in general move from species-centric initiatives to those focused on whole ecosystems, mycological research has become increasingly integrative and collaborative. The rise of molecular and bioinformatic subfields has brought about a revolution in our ability to identify and characterize fungi.

Coinciding with this explosion of tools and information has been a decline in the number of trained taxonomists, decreased funding for taxonomy, and a dearth of positions available for taxonomists entering the job market[149]. However, the incorporation of integrative taxonomy practices is reenergizing the field with both the incorporation of new tools for carrying out taxonomy and an expansion of the data types preserved and distributed by collections curators[6,150]. Examples include machine learning and MaldiTOF for automated species identification[151], microCT and 3D modeling for external and internal image analysis[152], GC-MS and HPLC metabolite profiling for chemotaxonomy[150], and genetic and genomic tools for phylogenetic placement and delineation (see Aime *et al.*[153] for a recent review on community standards for archiving diverse fungal taxonomy data). Whereas pitting molecular and computational methods for species identification against traditional mycology erodes collaboration and collective progress, integrative approaches promise to push the field forward while preserving organismal knowledge and well-developed tools.

To conserve and build fungal knowledge, we must also address systemic gaps in our knowledge base, such as geographic disparities in sampling and research. New fungal species descriptions come disproportionately from Europe, Asia, and North America, highlighting not only the volume of undescribed species from relatively well-characterized regions, but also geographic disparities in sampling, the uneven global distribution of taxonomists, the unintended impacts of restrictive export policies, and unequal access to scientific resources[154]. The preservation and characterization of fungi from undersampled geographic regions, particularly in known biodiversity hotspots, is critical to safeguarding fungal diversity. Local expertise from both professional and community scientists can go far to fill these gaps[124]. Local leadership is associated with greater long-term success of biodiversity and conservation initiatives[136]. Further, prioritizing capacity-building among local mycologists recognizes the experience of regional and indigenous people and builds resources at the local level where they are most likely to be used and built upon. Likewise, investment in local and indigenous expertise acknowledges the damaging roles of western colonialism and bio-appropriation in mycological research. Local collaboration should be structured around meaningful credited contributions, where regional experts are not just guides or sample collectors, but collaborators, contributors, authors, and research leaders. Facilitating fair international collaboration for biodiversity research is often mired in political and socio-economic issues. The Convention of Biological Diversities' Nagoya Protocol, which has been in effect since 2014, provides a framework for equitable benefit sharing of genetic resources and indigenous biodiversity knowledge and has facilitated protections and invaluable dialogue about research bioethics and ownership[154]. However, the Nagoya Protocol has been criticized for stifling both the advancement of local research as well as international research collaboration by privileging local government regulations that are at times directly responsible for the destruction of biodiversity, are often primarily concerned with the protection of natural resources perceived to be of economic interest, and do not necessarily distinguish between taxonomic and commercial research[155]. Describing and protecting biodiversity is necessarily connected to the socioeconomic concerns of local communities, and the success of long-term biodiversity programs depends on taking these concerns into account[136]. Protecting the rights of local communities while facilitating local capacity-building and international collaboration is being further complicated as lawmakers rush to incorporate genetic and genomic resources into provisions designed to address whole organisms[154,156]. The results of these policy decisions have important implications for mycological research in particular, due to the relatively small genome size and ease of sequencing relative to larger eukaryotes and the related amenability of fungi to high-mobility third-generation sequencing platforms like the Oxford Nanopore. These attributes provide loopholes to current laws, allowing researchers to extract genomic information onsite and thus avoid the transport of whole organisms across international borders.

Finally, but critically, the conservation of knowledge entails considering whose knowledge we are conserving, and who has been excluded. When last surveyed, the Mycological Society of America had a membership that was 85% white, with women underrepresented after the postdoc stage[157]. These numbers mirror those in other life science fields, where people of color, women, LGBTQAI, and disabled scientists are also unrepresented as they advance through the academic ranks[158]. The far-reaching effects of the loss of these individuals from the field cannot be overstated, and there is a profound need to recruit, truly support, and retain mycologists with diverse identities.

Concluding remarks

Preserving fungal diversity is imperative to protecting ecosystem functions, agricultural security, and human health. Mycologists have made significant progress illuminating species occurrence, function, and ecological relationships, but the bulk of fungal biodiversity is yet to be characterized. Accelerating fungal biodiversity research will require coordinated efforts including: amended frameworks for describing and tracking species; continued improvement in techniques and technologies for characterizing cryptic species; improvements in tools for linking functional diversity to genotypic diversity; preserving and engaging with fungaria and amending culture collection protocols and policy to recognize and preserve mixed substrates; preserving and standardizing diverse bodies of data and code, and the implementation of open science practices to all data sources including but not limited to methods, code, and cultures; building on the conservation practices (particularly at the ecosystem level) established in other systems with consideration for the barriers to conservation specific to fungi; ensuring the preservation of traditional mycological knowledge, while incorporating new tools for mycological progress; and the continued training and development of mycologists from diverse backgrounds, regions, and perspectives.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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