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YOUNG VOICES AND VISIONS FOR THE UN DECADE OF RESTORATION

REVIEW ARTICLE

The gap between mycorrhizal science and application: existence, origins, and relevance during the United Nation's Decade on Ecosystem Restoration

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During the United Nation's Decade on Ecosystem Restoration, planting material shortages are constraining restoration, while climate change exacerbates the need for restoration and reduces recruitment. Concurrently, research shows that native mycorrhizal fungi (symbiotic with plant roots) appropriate to plant provenance and site conditions significantly accelerate restoration, support crucial ecosystem services, and provide natural climate solutions (sequestering carbon), and nature-based solutions for climate change (climate adaptation). We reviewed 130 management plans for natural areas in the United States to evaluate whether restoring native mycorrhizal communities has translated into implementation. Although management plans frequently discussed the ecosystem services mycorrhizal fungi provide, nearly one half (46%) viewed fungi solely as pathogens or ignored them altogether. Only 8% of plans mentioned mycorrhizal fungi. Only one plan mentioned that mycorrhizae were potentially helpful to natural regeneration, while one other mentioned utilizing soil as a restoration tool. Our examination of publicly available data and case studies suggests that relatively meager protections for fungi, limited research funding and resulting data, research difficulty, and limited access to mycology experts and training contribute to this gap between science and implementation. A database of literature showcasing mycorrhizal ecosystem services and benefits is provided to highlight when and why mycorrhizae should be considered in management, regeneration, and restoration. Three action items are recommended to safeguard native mycorrhizal fungal communities and accelerate restoration and regeneration. Ten implementation tips based in scientific literature are provided to clarify the need and methods for mycorrhizal restoration.

Key words: ecosystem services, land management, mycorrhiza, natural climate solutions, nature-based solutions, restoration

Implications for Practice

- Native mycorrhizal fungi (symbiotic with plant roots) appropriate to plant provenance and site conditions meaningfully boost restoration outcomes, ecosystem services, natural climate solutions (carbon sequestration), and nature-based solutions for climate change (climate adaptation).
- Management plans overwhelmingly discuss the ecosystem services to which mycorrhizae contribute, but fail to mention mycorrhizal fungi, their conservation, or their utility.
- Closing this gap between mycorrhizal scientific knowledge and application could accelerate restoration and regeneration, and help mitigate climate change and planting material challenges.
- A database of mycorrhizal benefits is provided to assist identification of when and why mycorrhizae should be considered in management and restoration.
- Action items and implementation tips are provided to assist restoration practitioners and managers of natural areas.

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Introduction

As the United Nations' (UN) Decade on Ecosystem Restoration begins, studies suggest supplies of plant propagative material will constrain restoration (National Academies of Sciences, Engineering, and Medicine [NASEM] 2020; Fargione et al. 2021), while areas in need of restoration and regeneration will grow due to ongoing deforestation, shifting agriculture, and the increasing frequency and severity of extreme weather events (Curtis et al. 2018; NASEM 2020; Fargione et al. 2021). Simultaneously, climate change, and the associated increasing frequency and severity of extreme weather events, is reducing natural regeneration and recruitment by reducing seedling emergence, survival and fecundity, and purging belowground seed banks (Panetta et al. 2018; Costa dos Santos et al. 2019; Garnier et al. 2021). Mycorrhizal fungi, symbiotic with plant roots, provide a wide variety of services to plants and ecosystems, and offer a potentially crucial offset to the above challenges. For example, restoring native mycorrhizal fungal communities in conjunction with native plant communities can increase planting survival and establishment, native plant biomass, plant species richness, and site similarity to reference ecosystems (Rua et al. 2016; Koziol & Bever 2017; Neuenkamp et al. 2019; Policelli et al. 2020). Improvements of 30% or more in these and similar measurements of restoration success are not unusual when diverse mixes of native mycorrhizal fungi are paired with appropriate plants and site conditions (Koziol & Bever 2017; Neuenkamp et al. 2019).

Mycorrhizal restoration is necessary because disturbances including land use changes, invasive vegetation, pollution, reduced populations of native plant hosts, and herbicide application can negatively impact native mycorrhizal fungal communities in ways that can last for years (Meinhardt & Gehring 2012; Koziol & Bever 2017; Helander et al. 2018). In addition, mycorrhizal fungal communities found on plant propagative material may not be optimized to plant host or planting site conditions, even when specific attention is given to this step (Moreira et al. 2007; Sykorova et al. 2007; Southworth et al. 2009). For example, oak seedlings grown at a natural site and seedlings from the same site grown in a greenhouse shared none of the same taxa (Southworth et al. 2009). For these reasons, restoring native mycorrhizal fungal communities optimized for planting site and plant provenance (as an additional step to installing planting materials) could help offset other restoration, reforestation and land management challenges.

The management and restoration of mycorrhizal fungi is also appropriate on its own merit because mycorrhizal fungi provide ecosystem services that increase the function, resiliency, and positive impact of natural areas (Costanza et al. 1997). The benefits of mycorrhizal symbioses can be species, provenance, and context dependent (Rillig & Mummey 2006), and only a small subset of any mycorrhizal fungal community may provide a specific service (e.g. Egerton-Warburton et al. 2007). Yet, the scientific literature reveals many meaningful contributions of mycorrhizal fungi to ecosystem services. Figure 1 visually summarizes some of the ecosystem services mycorrhizal fungi can provide (left), and the corresponding results of their depletion (right). We summarize these ecosystem services below (additional details and references can be found in Supplement S1), before investigating whether there is a gap between the science of mycorrhizae and the implementation of that science in restoration and management.

Briefly, mycorrhizae can improve plant nutrition, build fertile soil, and improve moisture infiltration and retention in the soil (Supplement S1). Flower number and mass, nectar production, and seed production can be improved by mycorrhizae. Mycorrhizal hyphae and secretions cycle nutrients and aggregate soil. They protect against erosion, and reduce nutrient loss and leaching (Supplement S1). Contributions of mycorrhizae to ecosystem services also seem particularly relevant during the next decade as the climate changes. Mycorrhizae serve as natural climate solutions (increasing carbon storage; Griscom et al. 2017), by sequestering carbon underground in hyphae, competing with saprotrophs to reduce carbon release, and improving aboveground carbon storage via increased plant growth (see discussion in Baird & Pope Baird & Pope 2022). Mycorrhizae also act as nature-based solutions for climate change (natural means of adapting to climate changes; Nesshöver et al. 2017). By mediating plant water use and access, mycorrhizae improve plant drought resilience, water use efficiency, and cooling (Wu & Xia 2005). Mycorrhizae increase flowering duration, reducing potential timing mismatches between plants and pollinators under climate change (Barber & Gorden 2015; Supplement S1). While invasive vegetation and pests are expected to increase (Gregory et al. 2009; Clements & Ditommaso 2010), mycorrhizal fungi can boost plant defenses and reduce the presence and impacts of pests and pathogens (Reddy et al. 2006; Rinaudo et al. 2010; Supplement S1). Mycorrhizae can increase the nutritional value of food plants, which could counteract the declines expected with climate change (Avio et al. 2018; Bisbis et al. 2018). If common mycorrhizal networks are distributing resources underground as studies suggest (see Supplement S1 for references and discussion), they may also be improving ecosystem stability similar to the way spreading resources across a portfolio reduces the risk of financial investments (Schindler et al. 2015). Mycorrhizal fungal diversity also supports plant biodiversity and ecosystem productivity, and increases the efficiency of plant resource use (van der Heijden et al. 1998).

Although rarely studied, mycorrhizal contributions can cascade through ecosystems, influencing habitat quality and resource availability for other species. One study estimates that biomass in the Serengeti (including large carnivores) would be halved without the phosphorus supplied by mycorrhizal fungi (Stevens et al. 2018). Another study suggests that adding appropriate mycorrhizal inoculation to restoration for a 6.89 ha site would increase endangered bird habitat from 0 to 1.2 ha 6 years post-restoration (Tracy & Markovchick 2020).

Game et al. (2015) noted that there is frequently a gap between science and implementation in conservation. Thus, we questioned whether the utilization of mycorrhizal fungi as a restoration innovation had successfully bridged this gap. We hypothesized that usage of this tool may still be relatively

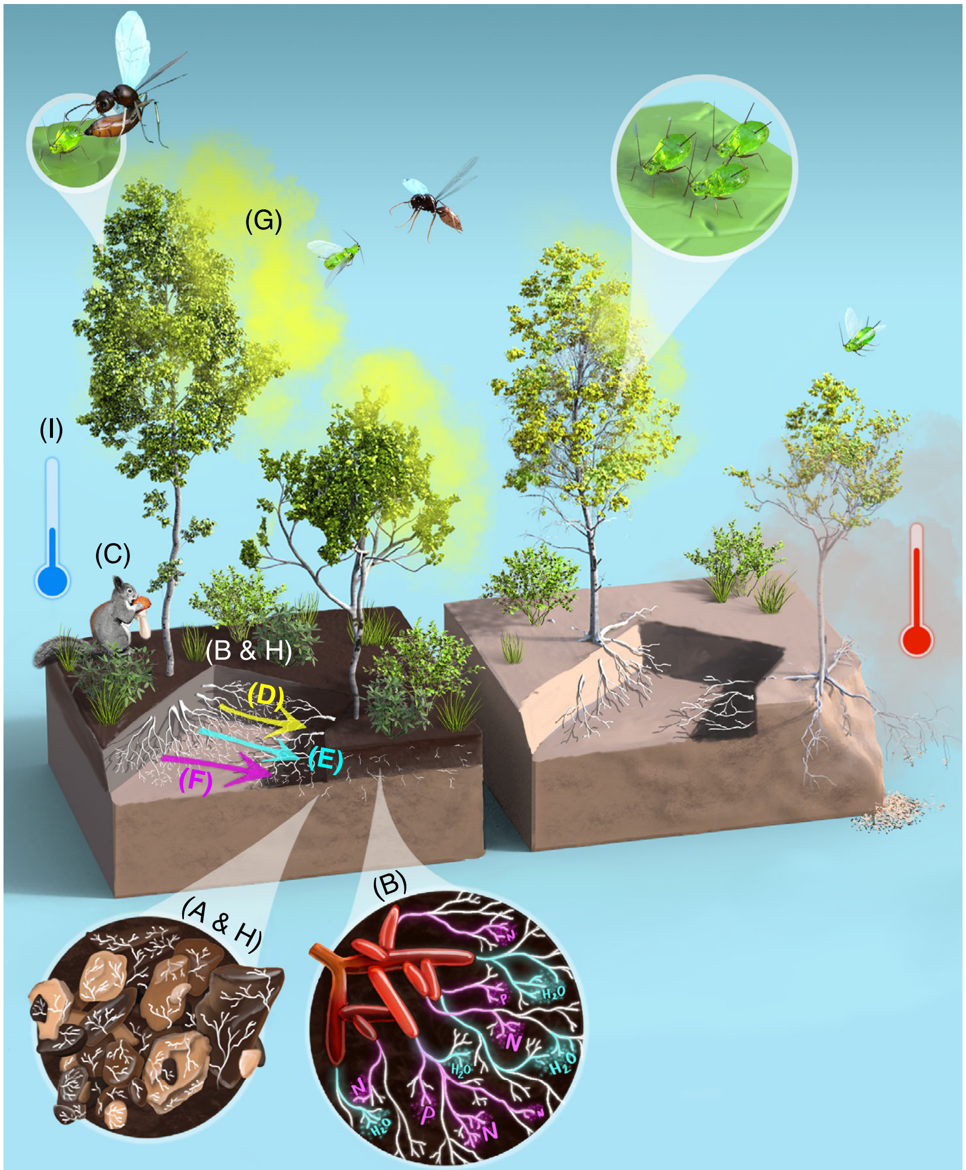

Figure 1. Examples of ecosystem services that can be provided by mycorrhizal fungi (left) and results of their depletion (right), including: soil aggregation preventing erosion and dust (A); nutrient and water mining improving plant nutrition, diversity, and resilience (B); additional food for mammals and insects (C); and common mycorrhizal networks that studies suggest are transporting nutrients (D), water (E), and pest warning signals (F) that enable advance and/or coordinated plant pest repellence and signaling of pest parasites, such as the aphids and their wasp parasites pictured here (G); increases in carbon storage in hyphal tissues and secretions belowground, and increased plant diversity, growth, resilience to stressors and canopy cover aboveground (H); reductions in temperature associated with additional plant diversity, growth, and resilience to stressors like drought (I). Illustration by Kara Gibson and Victor Leshyk.

uncommon outside academia. To investigate this issue, we examined natural resource management plans in the United States that were consistently available online from two different sources for their treatment of ecosystem services and mycorrhizae.

Review of Management Plans

We downloaded and methodically searched 130 national forest and grassland management plans, and state forest action plans. We chose these plans because they cover many acres of natural resources throughout the United States (over 853 million for state forest action plans, and over 97 million for national forest and grassland management plans), represent habitats populated by two of the most common types of mycorrhizal fungi (arbuscular mycorrhizal fungi [AMF]; ectomycorrhizal fungi [EMF]), and are consistently available for nearly all states and national grasslands and forests, avoiding bias due to inconsistent availability (National Association of State Foresters 2019; United States Forest Service [USFS] 2019). State forest action plans from the National Association of State Foresters ($n = 55$) were typically more recent, produced from 2008 to 2018 (with a median year of 2010), while plans downloaded from the U.S. Forest Service ($n = 75$) were slightly older, produced between 1984 and 2019 (with a median year of 2004).

Supplement S2 provides additional methodological details and the resulting database.

To evaluate each management plan's consideration of the life-sustaining ecosystem service categories outlined by Costanza et al. (1997), we searched each management plan ($n = 130$) for terms related to each ecosystem service category (Table 1) and reviewed occurrences to confirm the intent of the word usage. To evaluate the consideration of mycorrhizal fungi in each management plan, we systematically searched each plan ($n = 130$) for terms related to mycorrhizae (Table 2). Since very few plans mentioned mycorrhizae, we expanded the search to include terms related to multiple kinds of fungi (as in Table 2). Each occurrence was read to confirm its intent and categorize each mention with regard to its view of fungi (as described in Table 2 and Supplement S2).

Treatment of Ecosystem Services and Fungi in Management Plans

Management plans were often concerned with the same ecosystem services to which mycorrhizae contribute: 85–100% of the plans discussed 8 of the 10 ecosystem service categories ($n = 130$, Fig. 2; Supplement S2). Similar to a study in Australia that found 30% of national park management plans made no mention of fungi (Pouliot 2013; Irga et al. 2018), we found 22% of plans made no reference to fungi. Another 25% viewed fungi solely as a threat. This percentage is substantially lower than the 90% of plans that viewed fungi solely as a threat found by Pouliot in 2013, but still means that out of 130 management plans, nearly half (46%; 60 of 130) either completely ignored the entire Kingdom Fungi or viewed fungi only as a threat without any reference to their beneficial roles in

Table 2. The main questions addressed regarding the treatment of fungi in the sampled state forest action plans and national grassland and forest management plans, and the methods and search terms used to address them.

Questions addressed	*Search methods/terms*
(1) Are ecosystem services to which fungi contribute of concern in management plans? (2) If so, which ecosystem services are of concern?	Table 1 contains the ecosystem service categories considered. Each plan was searched for terms related to each ecosystem service category. Searches returned all words similar to search terms. Usage of terms was reviewed to confirm intent (e.g. "buffer" was not used in a mapping sense, but to refer to the ability of an area to buffer the effects of a disturbance)
(3) Are mycorrhizae mentioned in management plans? (4) Are fungi mentioned?	Each plan was initially searched for terms relating to mycorrhizae (with few results), and then for any terms relating to fungi, including: fungal, fungi, fungus; mycorrhiza, mycorrhizae, mycorrhizal; mushroom; endophyte; lichen; microbe, microbial, microbiome
(5) Do fungi appear in the plan as a threat; a resource, solution or indicator (RSI); or both?	For each plan, mentions of fungal terms were classified as a: (a) threat, or (b) resource, solution, or indicator (RSI). Plans that included both kinds of mentions were categorized as both

Table 1. Simplified ecosystem service (ES) categories used here, the original categories identified by Costanza et al. (1997), and the search terms used for each category. For manageability we focused on biological and life-sustaining categories (omitting cultural ecosystem services). Additional details on the methods used can be found in Supplement S2.

ES categories reviewed here	*Categories in Costanza et al. (1997)*	*Search terms used*
Disturbance regulation	Disturbance regulation	Adapt, adapting, adaptation, buffer, drilling, extreme weather, fire, flood, mining, natural disaster, natural hazard, plasticity, resilience
Climate	Climate regulation; gas regulation	Carbon credit, carbon sink, carbon market, carbon storage, climate change, climate regulation, sea level rise, sequester, carbon
Water	Water regulation; water supply; waste treatment	Clean water, filter, water availability, water quality, water quantity, water regulation, water supply, waste treatment
Habitat and biodiversity	Refugia	Biodiversity, biological diversity, ecosystem, endangered species, foundation species, protected species, restoration, species diversity, threatened species
Genetic resources	Genetic resources	Genetic(s), genetic adaptation, genetically adapted, genetic diversity, genetic exchange, genetic transfer, genetic variation
Nutrient cycling	Nutrient cycling; soil formation	Soil formation, soil quality, quality soil, soil productivity, fertile soil, nutrient cycle, nutrient cycling soil recycling, soil conservation, conserve soils, conservation of soil resources, ability of soil to hold nutrients, decomposition
Erosion control	Erosion control and sediment retention	Air quality, erosion, grazing
Pest regulation	Biological control	Bark beetle, disease, exotic, herbivory, invasive, pest
Pollination	Pollination	Pollinate, pollinator
Raw materials	Food production; raw materials	Agriculture, food, harvest, regeneration, succession, tree age, wood product

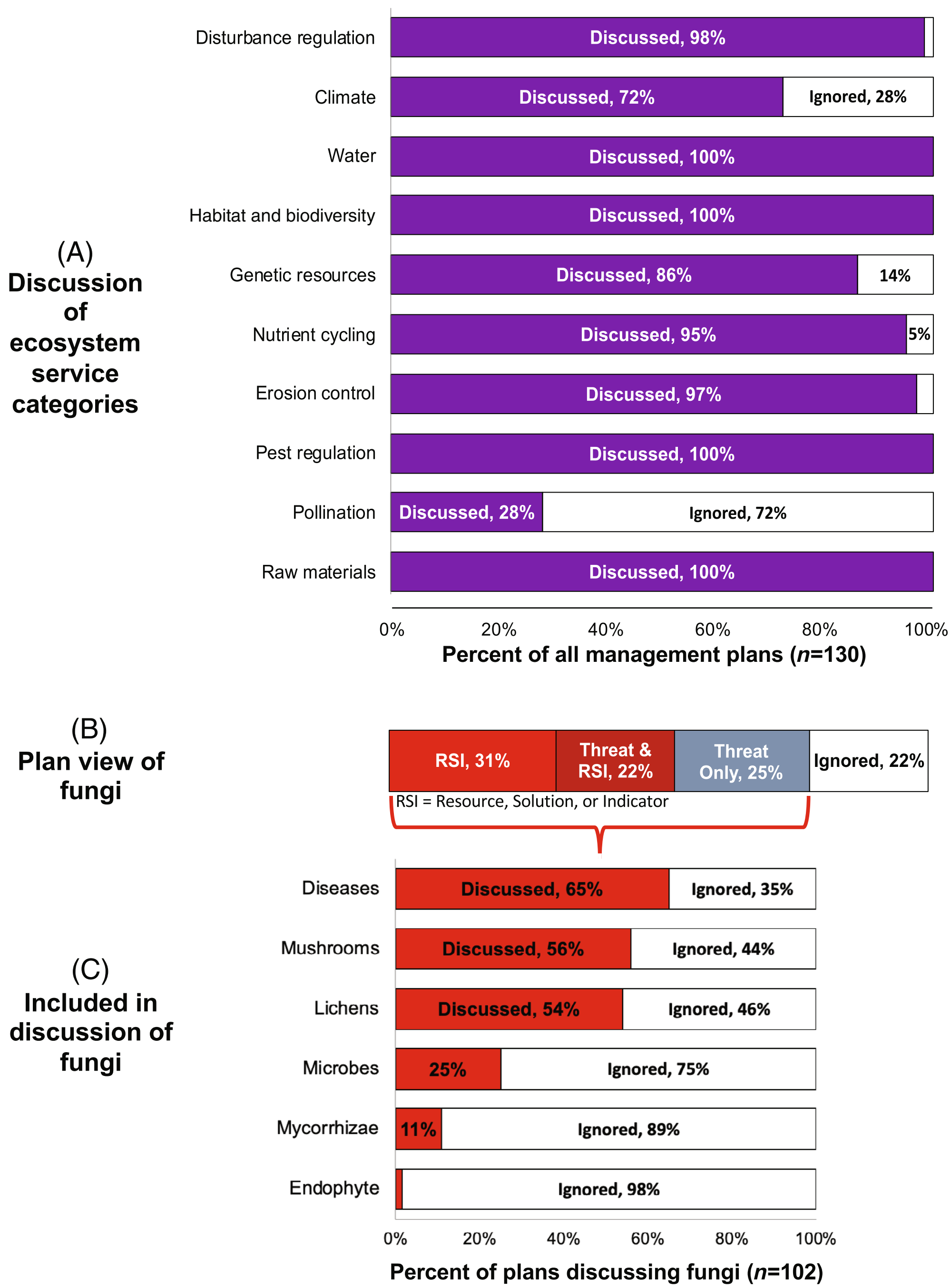

Figure 2. Results of systematically searching 130 management plans (National Association of State Foresters 2019; USFS 2019) for concern with individual ecosystem service categories and mycorrhizae (using terms found in Tables 1 and 2). Plans were largely concerned with the same ecosystem service categories to which mycorrhizae contribute (A). However, 46% of plans ignored the Kingdom of Fungi altogether or viewed fungi only as a threat (B). Few plans mentioned mycorrhizae, 8% of plans overall, and 11% of plans that mentioned fungi (C).

ecosystems, or their conservation. As Figure 2 shows, when management plans mentioned a fungal term ($n = 102$), it was most frequently due to disease (82%), mushrooms as food and harvestable items (56%), or lichens as air quality indicators and food for wildlife (54%). Plans that mentioned fungi only rarely mentioned mycorrhizal fungi (11%) or fungal endophytes (non-pathogenic/symbiotic fungi found inside plant tissues; 2%).

Nearly all plans (92%; and even 89% of those mentioning fungi) failed to mention mycorrhizae (Fig. 2), and only one plan specifically mentioned that mycorrhizae were potentially helpful to natural forest regeneration. One other plan mentioned utilizing soil as a restoration or regeneration tool. Of plans that mentioned mycorrhizae, most (91%) were from the U.S. Forest Service (with the exception of the Wisconsin Statewide Forest Strategy). We hypothesized that more recent plans would be more likely to mention mycorrhizae since the most convincing studies on the contributions of mycorrhizae to restoration and ecosystem services tend to be more recent. However, plans that mentioned mycorrhizae were developed between 1989 and 2015, with a median year of 2005 (similar to the median of 2004 seen for U.S. Forest Service plans overall). With the exception of the Wisconsin Statewide Forest Strategy, plans mentioning mycorrhizae were from the western United States and 36% fell under the Northwest Forest Plan Survey and Manage Guidelines which required the inclusion of fungi in monitoring and management (Molina 2008; Davoodian 2015).

Potential Causes of the Science-Application Gap

Few studies have evaluated disconnects between science and application for beneficial fungi, but those studies reveal that fungi are often ignored except as pathogens in public perception, university courses, and even by land managers and biologists (Pouliot 2013; Irga et al. 2018). To better understand the nature of this gap, we investigated factors we hypothesized could inhibit the translation of science on beneficial fungi into application. We examined the relative levels of legal protection and research funding, research difficulty and cost, and access to fungal expertise in restoration and land management contexts.

Relative Legal Protections and Research Funding

The presence of detailed knowledge and experts for specific taxa in the natural resources management workforce are frequently driven by the existence of legal protections such as the U.S. Endangered Species Act (ESA) and resulting funding. Thus, we hypothesized that poor legal protections and low levels of funding would represent barriers to mycorrhizal application in restoration and land management. To better understand the role legal protections might play, we systematically searched publicly available protected species lists for relative coverage of each Kingdom and compared this representation to the diversity of life represented by each Kingdom (Fig. 3; Supplement S3). Although estimates of the biodiversity of life across Kingdoms vary widely (Table S1; Supplement S3), fungi are an estimated 7% of the biodiversity on Earth with approximately 120,000 known taxa, and an estimated 97–99% remaining to be discovered (Hawksworth & Lücking 2017; Larsen et al. 2017; Fig. 3; Table S1). Yet, our systematic search of the International Union for the Conservation of Nature's (IUCN) Red List (2019) and ESA list (United States Fish and Wildlife Service [USFWS] 2019*a*) revealed that fungi are rarely mentioned in conservation listings (0–0.09%; Fig. 3; Supplement S3; Tables S2 & S3). In fact, commentary on the ESA reveals a lack of clarity surrounding the protections afforded to fungi by this crucial piece of legislation, despite the listing of multiple corals and two lichenized fungi under the act (Davoodian 2015; USFWS 2019*a*; Supplement S3). European reports focused on fungi with visible mushrooms (macrofungi) show similarly sparse protections, despite recent commitments to, and progress in, reviewing the conservation status of additional fungal taxa under the IUCN's Red List (Senn-Irlet et al. 2007; May et al. 2018; Supplement S3).

To investigate whether fungal research funding levels might also be contributing to the gap, we searched fiscal year (FY) 2018 federal research projects for mentions of different terms related to fungi and other organismal groups (Supplement S3; Tables S4 & S5). Although approximately 5% of FY2018 federal research projects that mention organismal groups include mentions of fungi, approximately 70% of this fungal research funding appears to relate to disease (Fig. 3). Fungal pathogens are serious threats, and their impact is expected to increase with climate change (Almeida et al. 2019). Yet, beneficial fungi are likely more numerous than fungal pathogens. For example, pathogenic fungi appear to constitute a small proportion of the fungal soil communities in North America compared to beneficial ectomycorrhizal and saprotrophic fungi (59 compared to 1988 taxa; Tedersoo et al. 2014). These beneficial fungi could be our allies against disease, pests, and stressors, including fungal pathogens, since many fungi produce antibacterial and antifungal compounds (Xu et al. 2015). Even fungi initially viewed as solely pathogenic are sometimes found to have beneficial qualities, such as producing key anticancer compounds and immunosuppressive therapies (Stone 1993; Watts et al. 2009). Yet, only 1.2% of U.S. FY2018 organismal research funding for projects that mention fungi refer to mycorrhizal fungi, for example.

Relative Research Difficulty and Cost

Given the complexity and often cryptic nature of fungal biology (tissues intermingled with symbionts, the difficulty of defining an individual, microscopic to vast underground sizes, etc.) we hypothesized that the difficulty and cost of fungal research might also lead to challenges translating science into management. The study of mycorrhizae frequently requires field collections, short- and long-term sample storage and curation, microscopy, genomic sequencing and stable isotope and mass spectral analyses (Lindahl et al. 2013), for example. Even questions of classification can be elusive. Species must often be defined statistically as a percentage of genomic sequence match, due to challenges associated with observing breeding behavior and other factors typically used for plants and animals (Lindahl et al. 2013). Additional complexity occurs because some fungi may not exist independently of their hosts, and fungal functions, persistence, and responses vary with changes in symbiont and environment (Rillig & Mummey 2006).

To evaluate mycorrhizal research difficulty and the role it could play in preventing effective translation of scientific promise to conservation and management, we quantified the differences involved in surveying for fungi versus plants using a case study from one of the authors (Fig. 4; Supplement S4). This example, surveys for an orchid, *Platanthera cooperi*, and its orchid mycorrhizal fungi (OMF), was chosen for three reasons. (1) It comes from a single project with consistent context and oversight such that extraneous costs and factors do not vary. (2) Searches for both plants and fungi must be carried out using methods specific to each. (3) Clear cost estimates exist for both

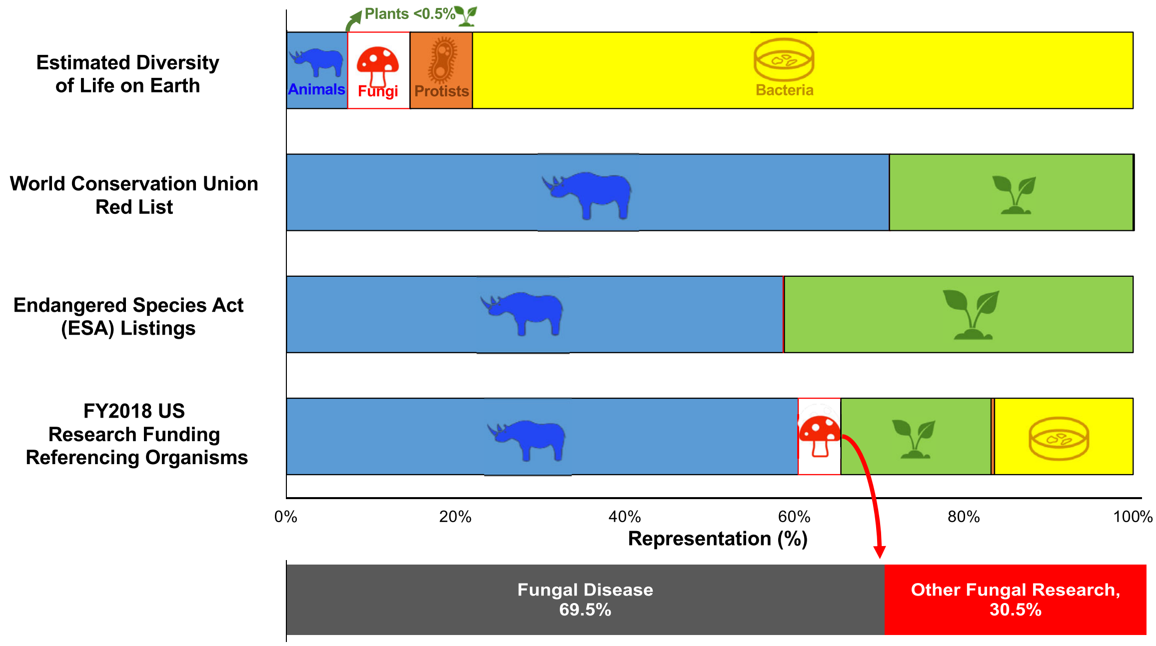

Figure 3. Relative representation of organismal groups within the estimated taxonomic diversity of life on earth (Larsen et al. 2017), International Union for Conservation of Nature Red List and U.S. Endangered Species Act conservation listings (IUCN and ESA, respectively; IUCN 2019; USFWS 2019*a*), and FY 2018 U.S. federal research funding referencing organisms (Star Metrics 2021). All organismal groups are represented in each series, but the representation of some groups is so small that they are not visible. Despite comprising 7% of the biodiversity on earth, fungi represent less than 0.1% of IUCN and ESA listings. Although fungi appear in 5% of 2018 U.S. federal research funding referencing organisms, 70% of this funding appears to target disease. Supplement S3 and Tables S1 through S4 contain additional details of diversity estimates, and protection and funding searches. Icons gratefully sourced from thenounproject.com.

the plant and mycorrhizal fungi portions of the project. The estimates provided focus on surveying the presence and identity of plant and fungal taxa, excluding other conservation and management actions. Results show that despite the crucial importance of OMF to the plant, there is a relative lack of information regarding OMF requirements concurrent with large disparities in survey cost and effort. Although the cost disparities outlined in this example do not represent all cases (see Supplement S4), it illustrates the challenges of understanding often more cryptic and poorly described fungal symbionts relative to their plant hosts.

Despite the understandable appeal of simply monitoring and managing the plant host alone, studies are clearly identifying the insufficiency of this approach. For example, restoration and regeneration (including range shifts in response to climate change) could depend entirely on the availability of appropriate fungal symbioses that may have been eliminated from the soil by invasive species, pollution, disturbance or herbicide application (Meinhardt & Gehring 2012; Helander et al. 2018). Koziol and Bever (Koziol & Bever 2017) found that some late successional plant species could not be restored without concurrent restoration of the appropriate mycorrhizal fungal community. Multiple studies indicate that appropriate pairings between plants, soil, and mycorrhizal fungi are key for beneficial results (Johnson et al. 1992, 2010; Rua et al. 2016). Both intraspecific and interspecific mycorrhizal diversity can be crucial to outcomes (van der Heijden et al. 1998; Johnson et al. 2012).

However, lower levels of regulatory protection and research funding can often lead to reduced levels of scientific knowledge, and have repercussions for implementation, reducing the information needed to translate science into application (Baird & Pope 2022). For example, information typically required for conservation and management of a taxon includes population sizes, distribution, and trends, and threats to the taxon (Table 3). These types of information often require repeated monitoring across time and a taxon's range, which often do not exist for fungal taxa, especially less visible taxa such as mycorrhizal fungi.

Relative fungal research funding levels are low, with 5% for fungi compared to 18% for plants, for example (Fig. 3; Supplement S3; Tables S2–S5). If relative fungal diversity (8% for fungi and less than 0.5% for plants; Fig. 3; Table S1) and the relative difficulty and cost of fungal research shown in Figure 4 (a potential ninefold difference, for example; Supplement S4) are considered in concert, relative funding for fungal research is even more incongruent (Supplement S5; Table S6). Decisions about the prioritization of research dollars require thorough consideration of societal values and the effectiveness of specific strategies, which we are not attempting here. However, we offer this example to inform efforts to translate science into application for beneficial fungi. For example, awaiting more thorough knowledge for implementation of mycorrhizal restoration (without meaningful changes in protections or research funding) could come with significant opportunity costs and loss of mycorrhizal diversity.

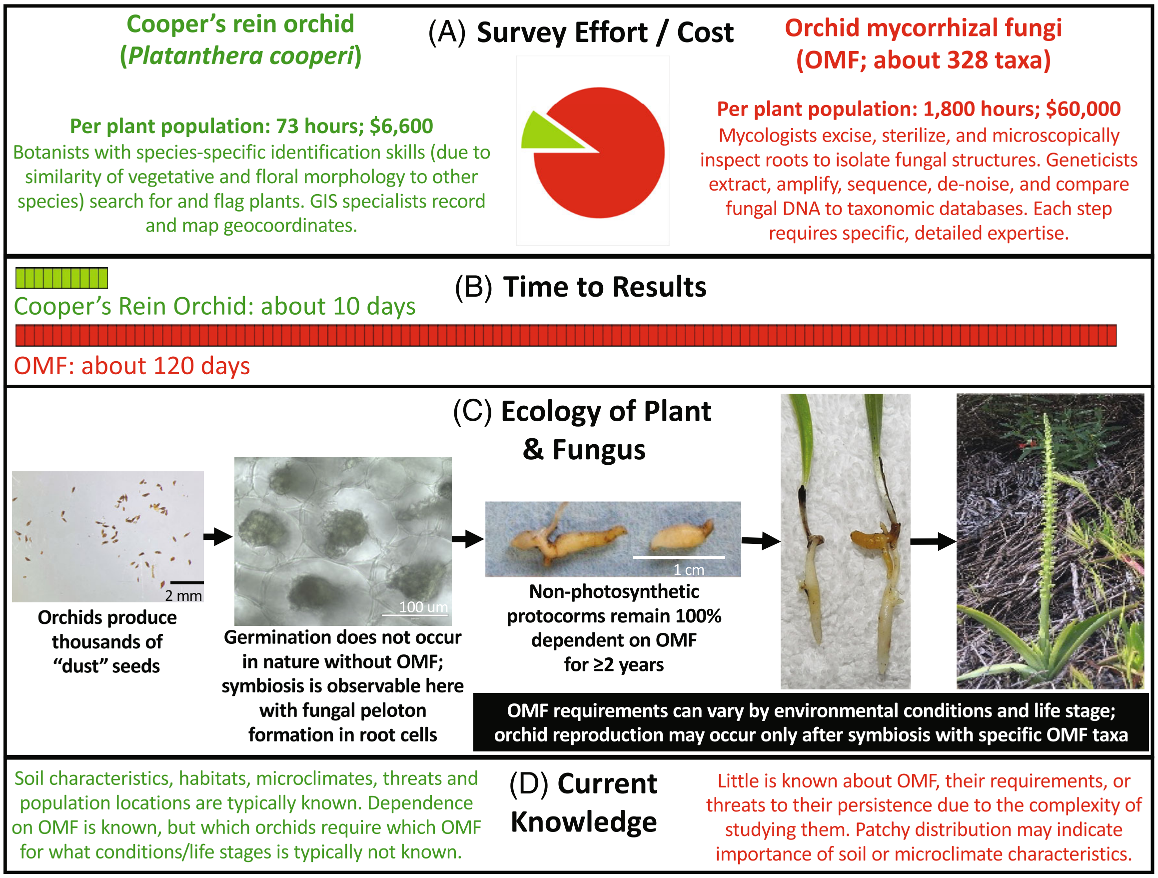

Figure 4. A case study comparing the relative effort and cost to survey (A), and time to obtain survey results (B) for a rare herbaceous plant and the beneficial OMF upon which it obligately depends. Investigations of orchids reveal orchid obligate dependence on OMF (C). However, relatively little is known about OMF requirements (D) concurrent with research cost and effort disparities (A, B). For additional details, see Supplement S4. Photos provided by Jyotsna Sharma.

Relative Access to Fungal Training and Expertise

Clear mandates for species protection and research funding often drive job and training availability, and the incorporation of experts into the practitioner workforce. To understand the presence of mycologists focused on beneficial fungi in the workforce, we examined the handbook of federal position classifications as a case study (United States Office of Personnel Management 2018). Although there is some overlap between categories, this examination reflects that of federal natural resources job classifications ($n = 30$), 33% relate to animals, 40% relate to plants, and only one category (3%) relates neutrally or positively to microorganisms broadly (covering fungi, bacteria, archaea and more). In contrast, at least two categories (6%) relate specifically to fungi as threats. The few studies we could locate that address this issue clearly state that mycologists and mycological knowledge are a relative rarity among natural resource managers (Molina 2008; Davoodian 2015; Irga et al. 2018), potentially stemming from historical distrust of fungi, and the difficulty of studying and defining them (Arora & Shephard Jr. 2008; Kaishian & Djoulakian 2020). For example, Molina (2008) and Irga et al. (2018) note that mycologists often do not have experience in restoration and management, and restoration and land management practitioners often have little access to mycologists.

The exception seems to have been the required integration of mycologists and mycology into land management under the Survey and Manage Standards and Guidelines of the Northwest Forest Plan (Molina 2008; Davoodian 2015). This effort ended with legal cases over the nature of integration between protections and industry. However, this effort resulted in 12 years of monitoring 9.7 million ha, yielding approximately 14,400 fungal records. This suggests great strides could be made in translating fungal research into application if organizations designated positions for mycologists specializing in beneficial fungi as they often do for botanists, physical soil scientists, and wildlife biologists (Molina 2008).

Reasons for Concern

The gap between mycorrhizal science and implementation would be less concerning if data suggested fungi were flourishing. However, many reports suggest fungi are in decline. The Survey and Manage Standards and Guidelines of the Northwest Forest Plan found that 55% of the 234 fungal taxa in the program were found at fewer than 20 locations, and 42% were found at 10 or fewer sites (Molina 2008). For comparison, the Eastern prairie fringed orchid (*Platanthera leucophaea*) is extant in

Table 3. Types of information typically required for conservation and management of taxa.

Source	*Information needed for conservation and management*
Endangered Species Act (USWFS 2019*b*)	• Current or expected habitat decline for the taxa • Overutilization data • Disease, pathogens, pests, parasites, and predators of the taxa • Existing regulatory mechanisms to protect the taxa • Degree, magnitude, location, and immediacy of threats to the taxa • Taxonomic distinctiveness
Red List categories and criteria (IUCN 2019)	• Taxa's population size, trends, and distribution • Fluctuations in the extent, occupancy, number of populations, or number of mature individuals in the taxa • Quantitative analysis of taxa's extinction probability
Managing protected areas, a global guide (De Lacy et al. 2006)	• Species inventories • Population size, trends, and distribution of the taxa • Habitat types and current conditions • Degree, magnitude, location, and immediacy of threats to the taxa • environmental services provided by the taxa

Table 4. Recommended action items in relation to mycorrhizae in natural areas, and tips for implementation. Expanded versions with additional context and references are available in Supplement S7.

Mycorrhizal action items for natural areas

(1) Manage for mycorrhizal fungi too, especially in areas with less historical disturbance that could act as mycorrhizal refugia and source populations, and in areas where events indicate restoration may be needed.
(2) When mycorrhizal restoration is indicated by prior land use or management, commit to restoring the full diversity of native mycorrhizal communities that are plant provenance appropriate and site appropriate.
(3) Develop mycorrhizal restoration plans alongside planting and natural regeneration plans and include mycorrhizal fungi in land management planning and documents. Address soil conservation concerns and measures for mycorrhizal restoration during planning.

Mycorrhizal implementation tips for natural areas

(1) Native mycorrhizal fungi meaningfully contribute to ecosystem services and land management goals.
(2) Both within and between species diversity of mycorrhizal fungi matter to outcomes.
(3) Native mycorrhizal communities may be depleted and degraded by a variety of disturbances.
(4) Fully functional, diverse native mycorrhizal communities often do not regenerate quickly.
(5) The needed native mycorrhizal communities are generally not present in sufficient numbers, combinations, or diversity on the plant material used in restoration.
(6) Inoculation of plantings with mixes of native mycorrhizal fungi optimized to plant provenance and site conditions, and representative of their diversity in nature, boosts restoration outcomes.
(7) Mass-produced mycorrhizal products can inhibit native mycorrhizae and yield poor results.
(8) Inappropriate plant/soil/mycorrhizal pairings and poor inoculation timing can lead to poor results.
(9) Optimal results are obtained with diverse mixes of native mycorrhizal communities appropriate to plant provenance and site.
(10) Successful inoculation requires direct contact with live mycorrhizae or activated spores.

59 populations and listed as threatened (USFWS 2019*a*), while its relative, the chaparral rein orchid (*Platanthera cooperi*) from Figure 4 is found at 162 locations and is considered vulnerable (The Calflora Database 2022). In Europe where there is a longer history of monitoring macrofungi (which form aboveground fruiting bodies, a category which includes many EMF), reports paint a similar picture, suggesting that many macrofungi are declining (Senn-Irlet et al. 2007). All 22 native species of hydnoid fungi (forming fruiting bodies with tooth-like projections) in The Netherlands and Northwestern Europe show declines in fruiting bodies since 1950 (Arnolds 2010), and fungal ethnoecology studies revealed that 53% of mushroom collectors in Poland report a steady decrease in macrofungi (Kotowski et al. 2021). The decline of mycorrhizal fungi generally is more difficult to assess because this category includes fungi that do not form large fruiting bodies aboveground, such as AMF. However, many studies report declines in mycorrhizal fungi due to various causes including land use change, invasive species, pollution, and herbicide use (Castellano & Gorchov 2012; Grove et al. 2012; Meinhardt & Gehring 2012; Swaty et al. 2016; Lilleskov et al. 2019). Ectomycorrhizal fungi (EMF), known to sequester more carbon than other types of mycorrhizal fungi, also appear particularly susceptible to climate change (Baird & Pope 2022).

In some cases, the dangers facing beneficial fungi mirror those for other species, and the same conservation strategies could benefit fungi (Minter 2011). For example, Clemmensen et al. (2013) found that habitat fragmentation, a common threat to biodiversity, is also a concern for mycorrhizal fungi and conservation mycology. Thus, conservation programs targeting the mitigation of fragmentation could benefit both charismatic taxa and lesser known taxa like mycorrhizal fungi. However, Cameron et al. (2019) documented geographic mismatches between terrestrial aboveground and soil (including mycorrhizal) biodiversity, finding that these mismatches cover 27% of the earth's terrestrial surface. Thus, efforts to protect areas of aboveground biodiversity may not sufficiently reduce threats to soil biodiversity (Cameron et al. 2019). In addition, even within areas that are protected, disturbances such as the treatment of invasive vegetation with pesticide (Helander et al. 2018), or self-reinforcing soil legacies left after invasion by exotic vegetation (Meinhardt & Gehring 2012), may quietly continue to reduce beneficial fungi, if these impacts are not recognized and specifically addressed as part of land management planning (Davoodian 2015; May et al. 2018; Willis 2018).

Implications for Research

Given the status and funding of fungal knowledge, it seems crucial to consider what kinds of fungal research could best support the translation of science on beneficial fungi into implementation. Here we focus on mycorrhizae. We suggest that research identifying mycorrhizal ecosystem service dollar values, and research explicitly exploring mycorrhizal effects on other ecosystem members, are crucial to informing a more widespread understanding of the costs and benefits of implementation. Costanza et al. (1997) argued that being aware of the dollar values of naturally provided ecosystem services aids in better decision-making. This is just as true for mycorrhizal fungi as for other taxa. Yet, a simplistic search could find no studies estimating the dollar values of mycorrhizal ecosystem services (Supplement S6). Thus, research on this topic offers a unique opportunity to contribute to our understanding of the world. Similarly, research regarding the links between mycorrhizae and benefits to protected areas or the success of protected or commercially valuable species could appropriately inform the conservation of multiple species and integrate mycological concerns with those of desired ecosystem services, nature-based solutions, and natural climate solutions. These types of research also lay a foundation for mycorrhizae to be considered in payment for ecosystem service and carbon credit programs (Fripp 2014; Senadheera et al. 2019), which could improve the conservation and restoration of mycorrhizal fungi while increasing ecosystem services and carbon sequestration, if the preservation of natural fungal diversity is also included as a goal.

Although we have focused on mycorrhizae here, it is clear that other trophic groups of fungi are similarly understudied and underserved. For example, endophytes were mentioned in management plans even less frequently than mycorrhizae, despite promising research on their contributions to host plant survival, growth, and defense (Moore et al. 2019; Yan et al. 2019). Our investigation of research funding and regulatory protections also revealed that levels of diversity and research funding for Archaea, Chromista, Protozoa, and Bacteria are similarly incongruent. Issues surrounding fungi with regard to regulatory protections and geographic mismatches between aboveground and belowground biodiversity (Cameron et al. 2019) seem similarly applicable to these other Kingdoms. Adequately covering these mismatches would require expertise and space well beyond this article. However, we have tried to provide examples of methods that could be utilized to identify and illuminate gaps between science and implementation, and inform efforts at narrowing those gaps, regardless of target taxa.

Conclusions and Implementation Tools

There is some good news for fungi. IUCN's Red List reviews of fungi are increasing (Supplement S3). Royal Botanic Gardens, Kew has issued inaugural (and follow-up) State of the World's Fungi reports and piloted civil scientists' use of mobile sample sequencing preparation technology (Harries 2017; Willis 2018). MycoFlora (2020) and MycoPortal (2020) pair community-based macrofungal specimen submissions with professional genomic sequencing. These programs do not address challenges associated with identifying fungal functions or more cryptic fungal forms, but they do represent important steps to reduce costs and increase available data (Dickinson et al. 2010; Irga et al. 2018).

Still, the difficulty and state of fungal science, relatively low levels of fungal protections and research funding, and the relative rarity of mycological experts among practitioners pose barriers to maximizing fungal contributions to management and conservation for all species. This is true 17 years after *Science* magazine's special issue focused on soils and fungi as the final frontier (Pennisi 2004).

Given the relative rarity of mycologists (Senn-Irlet et al. 2007; Irga et al. 2018), increasing links between land managers, restoration practitioners, civil scientists, and scientific experts (which has helped so many disciplines) seems particularly crucial for fungi (Minter 2011; Davoodian 2015). Improving integration has policy implications as well. For example, efforts to mandate and fund increased restoration and regeneration could include explicit calls for improved integration of appropriate mycorrhizal restoration. Policies protecting sensitive species and their habitats or requiring use of the best available science in land management, would seem to logically include science on the contributions and application of mycorrhizal fungi and other microbiota.

There is still much to learn about fungi and mycorrhizae. However, evidence is fairly clear regarding the efficacy of restoring fully diverse native mycorrhizal communities optimized to plant provenances and site conditions, and the failure of mass-produced fungal inoculants (Maltz & Treseder 2015; Rua et al. 2016; Neuenkamp et al. 2019). Evidence also seems fairly clear regarding declines in fungi, and the gap between science and implementation for mycorrhizae. To advance implementation, we developed three tools for restoration practitioners and land managers, included in the Supplemental Information (Supplements S1 and S7).

To empower practitioners to advocate for the assistance needed for implementation and enable examination of when and why it could be beneficial to include mycorrhizae in land management and restoration, we created a database of studies showcasing mycorrhizal ecosystem service contributions and restoration benefits (Supplement S1). The database lists examples by ecosystem service category, provides references for each example, and summarizes the treatments compared, type of effect, and magnitude of effect seen.

Based on the scientific literature, we recommend three mycorrhizal action items and 10 implementation tips for natural areas (in Table 4). The full versions of these tools include references and more detailed logic (Supplement S7). The mycorrhizal action items suggest three ways that restoration practitioners and managers of natural areas can benefit mycorrhizal fungi and the health of their ecosystems by considering mycorrhizae in their restoration and planning efforts. Baird and Pope (2022) also provide seven guidelines which complement these. The mycorrhizal implementation tips navigate and summarize some of the points we have discussed throughout this article, but in a condensed format specifically designed with practitioners in mind. We begin the implementation tips by highlighting the benefits that mycorrhizal fungi can provide and the importance of maintaining their full diversity (Supplement S1; van der Heijden et al. 1998; Johnson et al. 2012), step through the reasons why mycorrhizae need restoration, and summarize the evidence demonstrating what their successful restoration achieves (Meinhardt & Gehring 2012; Helander et al. 2018; Neuenkamp et al. 2019). We conclude the implementation tips with details to consider for appropriate and successful mycorrhizal restoration, including the poor performance and ethical considerations of mass-produced products, neutral to negative results seen with poor pairings (Maltz & Treseder 2015; Rua et al. 2016; Saloman et al. 2022), and other factors to consider to achieve successful inoculation (Supplement S7).

As the UN Decade on Ecosystem Restoration begins, appropriate mycorrhizal restoration could help offset restoration challenges, and represents a critical step toward re-orienting ecosystem restoration around whole ecosystems from the ground up.

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LITERATURE CITED

Almeida F, Rodrigues ML, Coehlo C (2019) The still underestimated problem of fungal diseases worldwide. Frontiers in Microbiology 10:214. https://doi.org/10.3389/fmicb.2019.00214

Arnolds E (2010) The fate of hydnoid fungi in the Netherlands and Northwestern Europe. Fungal Ecology 3:81–88. https://doi.org/10.1016/j.funeco.2009.05.005

Arora D, Shephard GH Jr (2008) Mushrooms and economic botany. Economic Botany 62:207–212. https://doi.org/10.1007/s12231-008-9046-3

Avio L, Turrini A, Giovannetti M, Sbrana C (2018) Designing the ideotype mycorrhizal symbionts for the production of healthy food. Frontiers in Plant Science 9:1089. https://doi.org/10.3389/fpls.2018.01089

Baird A, Pope F (2022) 'Can't see the forest for the trees': the importance of fungi in the context of UK tree planting. Food Energy and Security 11:e371. https://doi.org/10.1002/fes3.371

Barber NA, Gorden NLS (2015) How do belowground organisms influence plant–pollinator interactions? Journal of Plant Ecology 8:1–11. https://doi.org/10.1093/jpe/rtu012

Bisbis MB, Gruda N, Blanke M (2018) Potential impacts of climate change on vegetable production and product quality – a review. Journal of Cleaner Production 170:1602–1620. https://doi.org/10.1016/j.jclepro.2017.09.224

Cameron EK, Martins IS, Lavelle P, Mathieu J, Tedersoo L, Bahram M, et al. (2019) Global mismatches in aboveground and belowground biodiversity. Conservation Biology 33:1187–1192. https://doi.org/10.1111/cobi.13311

Castellano SM, Gorchov DL (2012) Reduced ectomycorrhizae on oak near invasive garlic mustard. Northeastern Naturalist 19:1–24. https://doi.org/10.1656/045.019.0101

Clements DR, Ditommaso A (2010) Climate change and weed adaptation: can evolution of invasive plants lead to greater range expansion than forecasted? Weed Research 51:227–240. https://doi.org/10.1111/j.1365-3180.2011.00850.x

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, et al. (2013) Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339:1615–1618. https://doi.org/10.1126/science.1231923

Costa dos Santos JF, Gleriani JM, Velloso SGS, de Souza GSA, do Amaral CH, Torres FTP, Medeiros NDG, do Reis M (2019) Wildfires as a major challenge for natural regeneration in Atlantic Forest. Science of the Total Environment 650:809–821. https://doi.org/10.1016/j.scitotenv.2018.09.016

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, et al. (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260. https://doi.org/10.1016/S0921-8009(98)00020-2

Curtis PG, Slay CM, Harris NL, Tyukavina A, Hansen MC (2018) Classifying drivers of global forest loss. Science 361:1108–1111. https://doi.org/10.1126/science.aau3445

Davoodian N (2015) Fungal conservation in the United States: current status of federal frameworks. Biodiversity and Conservation 24:2099–2104. https://doi.org/10.1007/s10531-015-0935-3

De Lacy T, Chapman J, Whitmore M, Worboys GL (2006) Chapter 10—Obtaining, managing, and communicating information. Pages 262–291. In: Lockwood M, Worboys GL, Kothari A (eds) Managing protected areas, a global guide. Earthscan, London, UK and Sterling, Virginia

Dickinson JL, Zuckerberg B, Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. Annual Review of Ecology, Evolution, and Systematics 41:149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Egerton-Warburton LM, Querejeta JI, Allen MF (2007) Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. Journal of Experimental Botany 58:1473–1483. https://doi.org/10.1093/jxb/erm009

Fargione J, Haase DL, Burney OT, Kildisheva OA, Edge G, Cook-Patton SC, et al. (2021) Challenges to the reforestation pipeline in the United States. Frontiers in Forests and Global Change 4:629198. https://doi.org/10.3389/ffgc.2021.629198

Fripp E (2014) Payments for ecosystem services (PES), a practical guide to assessing the feasibility of PES projects. Bogor, Indonesia. Center for International Forestry Research (CIFOR), Bogor, Indonesia. https://www.cifor.org/publications/pdf_files/Books/BFripp1401.pdf

Game ET, Schwartz MW, Knight AT (2015) Policy relevant conservation science. Conservation Letters 8:309–311. https://doi.org/10.1111/conl.12207

Garnier S, Giordanengo E, Saatkamp A, Santonja M, Reiter IM, Orts J-P, Gauquelin T, Meineri E (2021) Amplified drought induced by climate change reduces seedling emergence and increases seedling mortality for two Mediterranean perennial herbs. Ecology and Evolution 11:16143–16152. https://doi.org/10.1002/ece3.8295

Gregory PJ, Johnson SN, Newton AC, Ingram JS (2009) Integrating pests and pathogens into the climate change/food security debate. Journal of Experimental Botany 60:2827–2838. https://doi.org/10.1093/jxb/erp080

Griscom BW, Adams J, Ellis PW, Hougton RA, Lomax G, Miteva DA, et al. (2017) Natural climate solutions. Proceedings of the National Academy of Sciences 114:11645–11650. https://doi.org/10.1073/pnas.1710465114

Grove A, Haubensak KA, Parker IM (2012) Direct and indirect effects of allelopathy in the soil legacy of an exotic plant invasion. Plant Ecology 213:1869–1882. https://doi.org/10.1007/s11258-012-0079-4

Harries DJ (2017) DNA and the field mycologist: part 2. Field Mycology 18:92–96. https://doi.org/10.1016/j.fldmyc.2017.07.008

Hawksworth DL, Lücking R (2017) Fungal diversity revisited: 2.2 to 3.8 million species. Microbiology Spectrum 5:FUNK-0052-2016. https://doi.org/10.1128/9781555819583.ch4

Helander M, Saloniemi I, Omacini M, Druille M, Salminen J-P, Saikkonen K (2018) Glyphosate decreases mycorrhizal colonization and affects plant-soil feedback. Science of the Total Environment 642:285–291. https://doi.org/10.1016/j.scitotenv.2018.05.377

International Union for Conservation of Nature (IUCN) (2019) International Union for the Conservation of Nature Red List, version 2019-1. www.iucnredlist.org/ (accessed 18 April 2019)

Irga PJ, Barker K, Torpey FR (2018) Conservation mycology in Australia and the potential role of citizen science. Conservation Biology 32:1031–1037. https://doi.org/10.1111/cobi.13121

Johnson D, Martin F, Cairney JWG, Anderson IC (2012) The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. New Phytologist 194:614–628. https://doi.org/10.1111/j.1469-8137.2012.04087.x

Johnson NC, Tilman D, Wedin D (1992) Plant and soil controls on mycorrhizal fungal communities. Ecology 73:2034–2042. https://doi.org/10.2307/1941453

Johnson NC, Wilson GWT, Bowker MA, Wilson JA, Miller RM (2010) Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proceedings of the National Academy of Sciences of the United States of America 107:2093–2098. https://doi.org/10.1073/pnas.0906710107

Kaishian P, Djoulakian H (2020) The science underground: mycology as a queer discipline. Catalyst: Feminism, Theory, Technoscience 6:1–26. https://doi.org/10.28968/cftt.v6i2.33523

Kotowski MA, Molnár Z, Łuczaj L (2021) Fungal ethnoecology: observed habitat preferences and the perception of changes in fungal abundance by mushroom collectors in Poland. Journal of Ethnobiology and Ethnomedicine 17:29. https://doi.org/10.1186/s13002-021-00456-x

Koziol L, Bever JD (2017) AMF, phylogeny, and succession: specificity of response to mycorrhizal fungi increases for late-successional plants. Ecosphere 7:e01555. https://doi.org/10.1002/ecs2.1555

Larsen B, Miller EC, Rhodes MK, Wiens JJ (2017) Inordinate fondness of multiplied and redistributed: the number of species on earth and the new pie of life. The Quarterly Review of Biology 92:229–265. https://doi.org/10.1086/693564

Lilleskov EA, Kuyper TW, Bidartondo MI, Hobbie EA (2019) Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: a review. Environmental Pollution 246:148–162. https://doi.org/10.1016/j.envpol.2018.11.074

Lindahl BD, Nilsson RH, Tedersoo L, Abarenkov K, Carlsen T, Kjoller R, et al. (2013) Fungal community analysis by high-throughput sequencing of amplified markers—a user's guide. New Phytologist 199:288–299. https://doi.org/10.1111/nph.12243

Maltz MR, Treseder KK (2015) Sources of inocula influence mycorrhizal colonization of plants in restoration projects: a meta-analysis. Restoration Ecology 23:625–634. https://doi.org/10.1111/rec.12231

May TW, Cooper JA, Dahlberg A, Furci G, Minter DW, Mueller GM, Pouliot A, Yang Z (2018) Recognition of the discipline of conservation mycology. Conservation Biology 33:733–736. https://doi.org/10.1111/cobi.13228

Meinhardt KA, Gehring CA (2012) Disrupting mycorrhizal mutualisms: a potential mechanism by which exotic tamarisk outcompetes native cottonwoods. Ecological Applications 22:532–549. https://doi.org/10.1890/11-1247.1

Minter D (2011) What every botanist and zoologist should know—and what every mycologist should be telling them. International Mycological Association Fungus 2:14–18. https://doi.org/10.1007/BF03449489

Molina R (2008) Protecting rare, little known, old-growth forest-associated fungi in the Pacific Northwest USA: a case study in fungal conservation. Mycological Research 112:613–638. https://doi.org/10.1016/j.mycres.2007.12.005

Moore JD, Carlisle AE, Nelson JA, McCulley RL (2019) Fungal endophyte infection increases tall fescue's survival, growth, and flowering in a reconstructed prairie. Restoration Ecology 27:1000–1007. https://doi.org/10.1111/rec.12960

Moreira M, Nogueira MA, Tsai SM, Gomes-da-Costa SM, Cardoso EJBN (2007) Sporulation and diversity of arbuscular mycorrhizal fungi in Brazil Pine in the field and in the greenhouse. Mycorrhiza 17:519–526. https://doi.org/10.1007/s00572-007-0124-7

MycoFlora (2020) MycoFlora. www.mycoflora.org (accessed 23 July 2020)

MycoPortal (2020) MycoPortal. www.mycoportal.org (accessed 23 July 2020)

National Academies of Sciences, Engineering, and Medicine (NASEM) (2020) An assessment of the need for native seeds and the capacity for their supply: interim report. The National Academies Press, Washington, DC. https://doi.org/10.17226/25859

National Association of State Foresters (2019) Forest action plans. https://www.stateforesters.org/forest-action-plans/ (accessed multiple times throughout 2019)

Nesshöver C, Assmuth T, Irvine KN, Rusch GM, Waylen KA, Delbaere B, et al. (2017) The science, policy, and practice of nature-based solutions; an interdisciplinary perspective. Science of the Total Environment 579:1215–1227. https://doi.org/10.1016/j.scitotenv.2016.11.106

Neuenkamp L, Prober SM, Price JN, Zobel M, Standish RJ (2019) Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context, and time. Fungal Ecology 40:140–149. https://doi.org/10.1016/j.funeco.2018.05.004

Panetta AM, Stanton ML, Harte J (2018) Climate warming drives local extinction: evidence from observation and experimentation. Science Advances 4:eaaq1819. https://doi.org/10.1126/sciadv.aaq1819

Pennisi E (2004) The secret life of fungi. Science 304:1620–1622. https://doi.org/10.1126/science.304.5677.1620

Policelli N, Horton TR, Hudon AT, Patterson TR, Bhatnagar JM (2020) Back to roots: the role of ectomycorrhizal fungi in boreal and temperate forest restoration. Frontiers in Forests and Global Change 3:97. https://doi.org/10.3389/ffgc.2020.00097

Pouliot A (2013) Fungi and biodiversity conservation. Park Watch 253:26–27. https://search.informit.org/doi/10.3316/informit.493776294357176

Reddy BN, Raghavender CR, Sreevani A (2006) Approach for enhancing mycorrhiza-mediated disease resistance of tomato damping-off. Indian Phytopathology 59:299–304. https://citeseerx.ist.psu.edu/pdf/5b75c9b5b1112ada8b3af6e54eb7407f327d2031

Rillig MC, Mummey DL (2006) Mycorrhizae and soil structure. New Phytologist 171:41–53. https://doi.org/10.1111/j.1469-8137.2006.01750.x

Rinaudo V, Barberi P, Giovannetti M, van der Heijden MGA (2010) Mycorrhizal fungi suppress aggressive agricultural weeds. Plant and Soil 333:7–20. https://doi.org/10.1007/s11104-009-0202-z

Rua MA, Antoninka A, Antunes PM, Chaudhary VB, Gehring C, Lamit LJ, et al. (2016) Home-field advantage? Evidence of local adaptation among plants, soil, and arbuscular mycorrhizal fungi through meta-analysis. BMC Evolutionary Biology 16:122. https://doi.org/10.1186/s12862-016-0698-9

Saloman MJ, Demarmels R, Watts-Williams SJ, McLaughlin MJ, Kafle A, Ketelsen C, et al. (2022) Global evaluation of commercial arbuscular mycorrhizal inoculants under greenhouse and field conditions. Applied Soil Ecology 169:104225. https://doi.org/10.1016/j.apsoil.2021.104225

Schindler DE, Armstrong JB, Reed TE (2015) The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13:257–263. https://doi.org/10.1890/140275

Senadheera DKL, Wahala WMPSB, Weragoda S (2019) Livelihood and ecosystem benefits of carbon credits through rainforests: a T case study of Hiniduma Bio-link, Sri Lanka. Ecosysem Services 37:100933. https://doi.org/10.1016/j.ecoser.2019.100933

Senn-Irlet B, Heilmann-Clausen J, Genney D, and Dahlberg A (2007) Guidance for conservation of macrofungi in Europe. Prepared for the European Council for the Conservation of Fungi within the European Mycological Association. http://www.eccf.eu/Guidance_Fungi.pdf

Southworth D, Carrington EM, Frank JL, Gould P, Harrington CA, Devine WD (2009) Mycorrhizas on nursery and field seedlings of *Quercus garryana*. Mycorrhiza 19:149–158. https://doi.org/10.1007/s00572-008-0222-1

Star Metrics (2021) Federal RePORTER. https://federalreporter.nih.gov/ (accessed on 27 April 2021)

Stevens BM, Propster J, Wilson GWT, Abraham A, Ridenour C, Doughty C, Johnson NC (2018) Mycorrhizal symbioses influence the trophic structure of the Serengeti. Journal of Ecology 106:536–546. https://doi.org/10.1111/1365-2745.12916

The Calflora Database (2022) Calflora: Information on California plants for education, research and conservation, with data contributed by public and private institutions and individuals, including the Consortium of California Herbaria. https://www.calflora.org/ (accesses 20 January)

Stone R (1993) Surprise! A fungus factory for taxol? Science 260:154–155. https://doi.org/10.1126/science.8097059

Sykorova Z, Ineichen K, Weimken A, Redecker D (2007) The cultivation bias: different communities of arbuscular mycorrhizal fungi detected in roots from the field, from bait plants transplanted to the field, and from a greenhouse trap experiment. Mycorrhiza 18:1–14. https://doi.org/10.1007/s00572-007-0147-0

Swaty RL, Michael HM, Deckert R, Gehring CA (2016) Mapping the potential mycorrhizal associations of The United States of America. Fungal Ecology 24:1–9. https://doi.org/10.1016/j.funeco.2016.05.005

Tedersoo L, Bahram M, Põlme S, Koljalg U, Yorou NS, Wijesundera R, et al. (2014) Global diversity and geography of soil fungi. Science 346:1078. https://doi.org/10.1126/science.1256688

Tracy J, Markovchick L (2020) Using mycorrhizal fungi in restoration to improve habitat suitability for an endangered bird. RiversEdge West Riparian Restoration Conference, February 4–6. Grand Junction, Colorado, United States

United States Forest Service (USFS) (2019) Home: find a forest or grassland. https://www.fs.fed.us/ (accessed multiple times throughout 2019 to download management plans)

United States Fish and Wildlife Service (USFWS) (2019a) Environmental conservation system online. https://ecos.fws.gov/ecp0/reports/ad-hoc-species-report-input (accessed 18 April 2019)

United States Fish and Wildlife Service (USFWS) (2019b) US Fish & Wildlife Service endangered species listing and critical habitat overview. https://www.fws.gov/endangered/what-we-do/listing-overview.html (accessed 18 April 2019)

United States Office of Personnel Management (2018) Handbook of occupational groups and families. https://www.opm.gov/policy-data-oversight/classification-qualifications/classifying-general-schedule-positions/ (accessed 22 December 2019)

van der Heijden MG, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Weimken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72. https://doi.org/10.1038/23932

Watts R, Clunie G, Hall F, Marshall T (2009). Rheumatology. Pages 558. Oxford University Press, Cary, North Carolina and New York. https://books.google.com/books?id=1m_59s7Tt3UC&pg=PA558

Willis KJ (ed) (2018) State of the world's fungi 2018. Report. Royal Botanic Gardens, Kew. https://stateoftheworldsfungi.org/2018/reports/SOTWFungi_2018_Full_Report.pdf

Wu Q-S, Xia R-X (2005) Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well-watered and water stress conditions. Journal of Plant Physiology 163:417–425. https://doi.org/10.1016/j.jplph.2005.04.024

Xu L, Meng W, Cao C, Cao C, Wang J, Shan W, Wang Q (2015) Antibacterial and antifungal compounds from marine fungi. Marine Drugs 13: 3479–3513. https://doi.org/10.3390/md13063479

Yan L, Zhu J, Zhao X, Shi J, Jiang C, Shao D (2019) Beneficial effects of endophytic fungi colonization on plants. Applied Microbiology and Biotechnology 103:3327–3340. https://doi.org/10.1007/s00253-019-09713-2

Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Studies showcasing contributions by mycorrhizal fungi.
Supplement S2. Details for systematic search of management plans.
Supplement S3. Methods for fungal protection and funding searches.
Supplement S4: Cost analysis for orchid and OMF (Fig. 4).
Supplement S5: Methods for comparing fungal and plant funding.
Supplement S6: Search results for terms in *Ecosystem Services* articles.
Supplement S7: Tools for restoration practitioners and managers of natural areas.
Table S1. Wide-ranging estimates of biodiversity across the Kingdoms of life.
Table S2. Results of protection and funding searches used to create Figure 3.
Table S3. Results of IUCN Red List search.
Table S4. Search terms and results by organismal group for fiscal year 2018 research projects.
Table S5. Search terms and results from searching fiscal year 2018 research projects for fungal subgroups.
Table S6. FY2018 fungal research funding equivalent to that for plants, if diversity and difficulty were included.
Figure S1. GoogleScholar™ search results (5 January 2022) for *Ecosystem Services* journal articles containing "dollar" (top; 226 results) versus "dollar" and mycorrhizal terms (bottom; 3 results).

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