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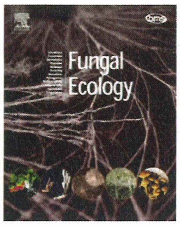

Addressing uncertainty: How to conserve and manage rare or little-known fungi

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ABSTRACT

One of the greater challenges in conserving fungi comes from our incomplete knowledge of degree of rarity, risk status, and habitat requirements of most fungal species. We discuss approaches to immediately begin closing knowledge gaps, including: (1) harnessing collective expert knowledge so that data from professional experiences (e.g., personal collection and herbarium records) are better organized and made available to the broader mycological community; (2) thinking outside the mycology box by learning and borrowing from conservation approaches to other taxonomic groups; (3) developing and testing hypothesis-driven habitat models for representative fungi to provide support for habitat restoration and management; (4) framing ecological questions and conducting field surveys and research more directly pertinent to conservation information needs; and (5) providing adaptive management guidelines and strategies for resource managers to conserve fungi based on incrementally improving knowledge from experience and conservation research.

Introduction

The workshop on conservation of fungi at the 2009 Mycological Society of America meetings in Snowbird, Utah posed this question: Have we enough information to make sound conservation judgments and management recommendations for fungi at risk or fungi in general? The answer was an equivocal yes and no. Yes, knowledge of taxonomy, biology, and ecology of fungi is considerable and growing rapidly with use of molecular tools. Yet, we remain daunted by the number of fungus species about which we know little or nothing, not to mention those still undiscovered. Much of the data, particularly on species occurrences and geographic ranges, and ecology remain disparate and difficult or impossible to obtain for systematic rarity and risk analysis. Collection data often lack essential information for species or fungal communities, e.g., detailed macro- and microhabitat requirements or population metrics. Such knowledge and data gaps produce great uncertainty in identifying species at risk and appropriate conservation measures. Nevertheless, rather than discouraging mycologists, this raises an exciting challenge.

Conservation of fungi raises several key questions. Do we include all fungal species in a conservation agenda or only rare species? If we focus on rare species, how do we determine which are truly rare? Fungi are difficult to detect due to their

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often cryptic natures and ephemeral production of fruiting structures. Of the *ca.* 1.5 million estimated species, only about 5 % are formally described (Hawksworth 1997, 2001). Although mycologists have determined through Red-list analyses that several hundreds are indeed rare (Dahlberg *et al.* 2009), most fall into what Molina & Marcot (2007) called the "little-known conundrum" – some may indeed be rare, others common, but we do not know about rarity for most and likely will never know. Further, we know that fungi play key functional roles in nutrient dynamics (Talbot *et al.* 2008), soil health (Claridge *et al.* 2009a), species mutualisms and interactions (Nishida 2007; Mack & Rudgers 2008), and overall ecosystem processes (Dighton *et al.* 2005), but without knowledge of distribution and ecology of fungal species and communities in specific environments, developing effective conservation guidelines will be difficult.

How then do we conserve such an extremely diverse group for which so much knowledge is lacking and difficult to obtain? Clearly we cannot protect all fungi on a species-by-species basis. Yet, much of fungal conservation *via* the IUCN is species-based. To be inclusive for conserving fungi in general (i.e., all the rare or little-known species), we need to test broader system-level approaches (Raphael & Molina 2007).

We do not review here all the issues regarding conservation of fungi. Instead, we highlight some key areas where mycologists can have immediate and positive impact on producing more data and designing studies that address critical knowledge gaps and uncertainty. We focus on three common themes. First, recognize that we will never have the complete knowledge that is needed to address the issues surrounding fungus conservation especially at the species-specific level. Second, mycologists need to think outside the mycology box, consider conservation efforts of other disciplines, and seek opportunities to test approaches and principles developed for other taxa or systems. Third, mycologists can help craft fungus conservation guidelines in an adaptive framework that tests their efficacy and incrementally adds knowledge. We draw on examples from the literature and practical experience with conservation efforts in the Pacific Northwestern USA, particularly for ectomycorrhizal (EM) fungi.

Sources of uncertainty

Prioritizing information needs first entails understanding the basic sources of uncertainty for conserving rare or little-known species. Molina & Marcot (2007) described three overlapping categories of such uncertainty:

(1) *Taxonomic uncertainty* – The primary source is the great number of species, most of which remain undiscovered or undescribed, and the frequent morphological similarity of taxa that are genetically distinct. Progress comes relatively slowly in fungal systematics due to an eroding cadre of trained taxonomists, loss of potential new taxonomists among graduate student ranks to molecular disciplines, and lack of monographs and identification keys. Even though molecular studies have illuminated the evolution and phylogeny of fungi, there is a downside to some degree regarding species identifications – some ecological diversity studies determine only unique DNA sequences, simply referred to as "taxonomic units," and we are left with poor description of the actual species involved.

(2) *Distributional uncertainty* – We lack systematic inventories of fungal species presence, abundance, and distribution – all key determinants of species rarity, population trends, and extirpation risk. Inventories or systematic surveys are difficult for several reasons, including lack of experts to identify specimens (related to 1 above), training of field crews in fungal collection, multiple years of surveys to document presence or absence, and overall expense. Most surveys focus on macrofungus sporocarps, but numerous molecular studies indicate that sporocarp surveys typically underestimate diversity and do not accurately reflect species abundance or dominance in soils or roots (Horton & Bruns 2001). Successful examples of large-scale fungal surveys or inventories (Ehlers *et al.* 2003; Molina 2008) and availability of inventory tools (Mueller *et al.* 2004) indicate that we can progress significantly here if we design the studies according to appropriate statistical sampling and established collection protocols.

(3) *Ecological uncertainty* – Molecular tools have provided a wealth of new information on fungal diversity, community dynamics, host specificity, and species interactions. Yet, we lack critical information on environmental associations and habitat requirements for most fungi at micro- and macrohabitat scales. We poorly understand responses of most fungal species to natural and anthropogenic disturbance at small and large spatial and temporal scales (e.g., Penttila *et al.* 2006; Peay *et al.* 2007; Trappe *et al.* 2009b,c). Ecological information is needed to develop effective management guidelines that maintain or restore habitat for fungal species. Species conservation programs typically take into account population trends, yet we lack critical population metrics and methods for fungi, such as defining individuals and their longevity, dispersal modes and capabilities, and genetic structure. Further, mycologists need to understand how fungi have adapted to past changes in the environment at various spatial and temporal scales so that we can predict response to ecosystem changes, including climate change (e.g., Chung *et al.* 2006).

Given these many uncertainties, how can mycologists better foster conservation guidelines and craft research approaches to improve our ability to conserve fungi in the long term?

Harnessing expert knowledge

Mycology has a long history of excellence in field collection by regional experts, often senior professors at universities with long-lived mycology programs, as well as by a cadre of talented non-professionals in mycological societies around the world. Much of our knowledge on the occurrence and natural history of fungi lies within the personal experience and unpublished records of these experts and is often unavailable to the wider scientific community. This untapped reservoir of knowledge is needed to deal with challenges of fungus conservation.

Digitizing collection data and making it publicly available can solve much of the problem of personal collection data. For example, many fungal herbaria have digitized data from herbarium labels, often from personal collections that have been accessioned, and made that data available on-line. Digitizing collection data can be expensive, but the data are immensely valuable in conservation programs. Mycological societies need to include that in their conservation agendas – how best to collate and organize disparate fungal databases of field collections to make them useful for conservation analyses?

Expert knowledge makes its largest impact when targeted towards a specific conservation or management objective. For example, Redhead (1997) produced the first comprehensive analysis of the biodiversity and conservation status of the macrofungi of British Columbia. His report was part of the provincial government's efforts to develop publications "to increase awareness and understanding of biodiversity" and "promote the concepts and importance of conserving biodiversity." In addition to reviewing available literature and analyzing regional data, Redhead clearly brought his vast experience of fungi in the region to bear on the problem, particularly by listing several potentially rare species and identifying forest regions of conservation concern for fungi. Similarly, Trappe *et al.* (2009a) summarized decades of personal knowledge on the diversity and ecology of hypogeous fungi (truffles) in forests of the Pacific Northwestern USA. They provided the first comprehensive list of truffle species, their rarity status, and conservation considerations. Like RED-lists, such regional analyses by resident experts provide the foundation for identifying species at risk and areas of needed inventory and research.

Expert knowledge proves most practical when mycologists collaborate with resource managers and apply their joint expertise to a management problem. A working example from the Pacific Northwestern USA follows. There, several expert mycologists engaged in a regional conservation program that eventually included protection for several hundred fungi (Molina *et al.* 2006; Molina 2008).

Conserving fungi under the Northwest Forest Plan

In 1993, federal forest managers and scientists were required by court order to develop a regional Northwest Forest Plan (NWFP) to protect species, including macrofungi, associated with old-growth forests. Expert panels were organized for the various biological groups of concern; each panel was instructed to provide their collective expertise on species and habitats that might require conservation attention, and conservation guidelines that could be used by forest managers. The macrofungus expert panel consisted of Prof. Joe Ammirati of the University of Washington, Department of Botany, Prof. Bill Denison of the Oregon State University, Department of Botany and Plant Pathology, and Prof. Jim Trappe of the Oregon State University, Department of Forest Science. Together they represented some 70 person-years of collecting, studying and teaching about the fungi of the Pacific Northwest. They also used data collected by their students, amateurs, and amateur societies such as the North American Mycological Association, North American Truffling Society, and regional mycological clubs such as the Oregon Mycological Society. The panelists were encouraged to consult with mycologists at other institutions and agencies having experience with the region's macrofungi.

The macrofungus panelists were instructed to identify rare, endemic, or threatened macrofungus species that are, or might be, closely associated with old-growth forests in the region. The panel results had to be defensible in court, should they be legally challenged. The criteria for their species selection were to be based on: (1) published research or listings; (2) herbarium records; (3) nominations from other mycologists; and (4) panelists' personal experience in collecting and identifying species. Criterion 1, published sources, was a good starting point, especially for described taxa apparently endemic to the Pacific Northwest. Criterion 2 was less useful: identifications of herbarium specimens were not always accurate, and the collections tended to be dominated by taxa of special research interest to the past and present mycologists associated with those herbaria. Moreover, Dr. Nancy Weber, who provided invaluable information to the panel *via* personal communications, discovered an interesting phenomenon: judging species rarity from herbarium records was often wrong. Very common species, such as *Aleuria aurantia*, would be judged as rare because they were so common they were seldom collected and even more seldom accessioned into herbaria. The truly rare taxa, in contrast, would appear to be relatively common, because when encountered by a knowledgeable collector, they usually would be picked and accessioned into herbaria simply because they were rare. Criteria 3 and 4 were especially useful to the panel.

At its first meeting, the macrofungus panelists developed their assessment procedures and divided their primary responsibility for different groups: Ammirati for epigeous Basidiomycota, Denison for epigeous Ascomycota, and Trappe for all hypogeous taxa. They then returned to their home institutions to consult with colleagues and collectors, search the literature, check their institutions' herbaria, and explore their own collecting records in detail. It soon became evident that undescribed and unnamed taxa in the panelists' working herbaria would be prominent among those that merited the "rare" status. All common taxa likely had been found and described, but rare taxa often had not been described and were represented by only one or two collections. This was particularly true with hypogeous fungi.

After sharing their lists by mail, they reconvened. At that stage some taxa thought by one panelist to be associated with old-growth forests had been found by other panelists to be common in young forests elsewhere, or one proposed as rare by a panelist proved to be common in habitats more familiar to another panelist. Or, a taxon not on the rare list in one panelist's group was proposed to be rare by another panelist. This sharing of information resulted in a final list of 234 macrofungal species that the panelists agreed could be defended in court.

Subsequent collecting by surveys organized within the NWFP's Survey and Manage Species Conservation Program (SMSCP), and by gathering of additional information under the NWFP's Annual Species Review process, resulted in some taxa being removed from the protected status list. For the most part, however, the panelists' conclusions have withstood the test of time (Molina 2008).

Thinking outside the mycology box

The literature on species conservation biology and management is extensive and mycologists are relative newcomers. So it is important that mycologists take advantage of conservation methods and approaches developed for other taxa and ecological communities. Given the large number of rare species likely needing protection worldwide, and limited management resources to provide protection, there has been extensive debate in the literature on whether we should focus on individual species (i.e., species or fine-filter approaches) or on protecting species assemblages and ecosystems (i.e., system or coarse-filter approaches). Marcot & Flather (2007) and Marcot & Sieg (2007) reviewed 33 conservation approaches (12 species and 21 systems, respectively) and their efficacy for protecting rare or little-known species, summarized as follows.

Species approaches

Species approaches typically target individual species at risk, manage known locations, and can use conservation strategies based on analyses of population viability. Approaches can also focus on surrogate species (e.g., indicator, umbrella, flagship species) that reflect the needs of other species with the underlying premise that if the surrogate is protected so too are its associated species. Pros: specific locations of known rare species receive immediate protection; knowledge of population dynamics provides a scientific foundation to conserve species; and cost may be reduced if indeed protection of a surrogate provides protection for a larger suite of species. Cons: it may be difficult to locate and protect all sites of a rare species; we lack comprehensive population data for viability analysis; and surrogate species may not be reliable indicators.

Systems' approaches

Systems' approaches include identifying biodiversity hotspots or establishing reserves for biodiversity protection; focusing on the range of natural variation in system structure, composition, or disturbance regimes wherein managers try to maintain or restore system structure and composition by emulating natural disturbance regimes; maintaining a diversity of habitat conditions such as a mix of successional stages and plant communities across a landscape; maintaining and monitoring ecosystem processes such as nutrient cycling, food webs, and key ecological functions of the target species group; and maintaining or conserving indicators of system status such as keystone species or certain functional groups. Pros: established reserves and use of system indicators can provide general protection for multiple species; and rare or little-known species may find suitable resources and habitat in landscapes managed within historic disturbance regimes and natural variation. Cons: establishing reserves may not be possible in all geographic locations and some species may not occur in reserves; indicator approaches may not be reliable for many species; we poorly understand response of many fungi to various types of disturbance that may be used to maintain or restore habitat.

Given the complexities and expense of species conservation worldwide, a blend of species and systems approach will likely be needed (Hansen *et al.* 1999; Kintsch & Urban 2002; Noon *et al.* 2003; Hunter 2005) particularly for species groups such as fungi with many little-known species (Raphael & Molina 2007). Combining approaches allows for protecting species-specific locations where such knowledge exists and providing continuity of natural system conditions and dynamics. The SMSCP used such a blend combining protection afforded by maintaining known sites, delineating a system of old-growth forest reserves across the planning area, and managing forests to rebuild old-growth forest structure and function (Molina 2008).

The IUCN Red-listing process and protection of reserves have received attention in the mycological literature as important approaches to fungus conservation (Moore *et al.* 2001; Dahlberg *et al.* 2009), but the various species and system approaches summarized above provide many other options for mycologists to consider. For example, in fungal community studies, can we identify fungal species that indicate presence of a larger suite of fungi, including rare species? Jumpponen *et al.* (2004) combined association analysis with habitat modeling to explore the potential of indicator species and specific suites of hypogeous fungi to associate with each other and with an array of habitat characteristics. They concluded that most taxa had evolved individual habitat requirements that thwart definition of consistent fungal communities by association analysis. Still, some individual species consistently associated with each other in certain habitats, and others were significantly negatively associated. These and other results not outlined here opened up a variety of possibilities for use of indicator species, fungus associations, or habitat associations to signal likely occurrence or absence of certain other species.

Similarly, from a systems perspective, do some fungal species indicate important fungal ecosystem functions (e.g., key food web interactions, nitrogen mobilization)? If we manage systems to emulate natural disturbance regimes (e.g., promote specific fire-return intervals) will fungi, including rare species, reoccupy new habitat? Will others disappear if fire is excluded for extended periods? Use of systems approaches may carry higher levels of uncertainty than species approaches for conserving species, particularly rare species, but they may also provide our best opportunity to conserve fungal communities at regional scales and to integrate conservation of fungi with conservation of plant and animal taxa and ecosystems. Both species and systems conservation approaches require a better understanding of fungal habitat.

What is "fungal habitat"?

Mycologists have voiced a clear consensus that conservation of fungi must include protecting "habitat" (Watling 1997; Moore *et al.* 2001). Yet we lack an operational definition of fungal habitat. Herbarium labels often contain only simple and vague habitat descriptors such as grassland, meadow, woodland, hardwood forest, or mixed conifer forest, which lack the detail needed to develop habitat management guidelines. So what do mycologists mean by "habitat"? Hall *et al.* (1997) emphasized that "habitat is organism specific; it relates the presence of a species, population, or individual (animal or plant) to an area's physical and biological characteristics". They defined habitat as "the resources and conditions present in an area that produces occupancy – including survival and reproduction – by a given organism." Thus, habitat is not static (e.g., a specific vegetation type) but dynamic in space and time, particularly for fungi where resources such as nutrient pools or growth substrates can quickly vary. Understanding the dynamic nature of fungal habitat will be key to predicting how anthropogenic or natural changes in ecosystems will provide habitat for rare or at-risk fungi. Developing a generalized framework that defines habitat for fungi, including key biological and environmental metrics, is a potential task for mycological societies as they develop a conservation agenda.

Habitat modeling provides tools and processes to define habitat and aid development of management guidelines. Approaches to habitat modeling abound, and we will discuss a few examples (see Marcot & Molina 2007 for a review on habitat modeling for rare or little-known species). One approach to habitat modeling can entail combining knowledge from experts (e.g., Geneletti 2005; Carter *et al.* 2006). For example, as part of the SMSCP, Marcot (2006) developed a Bayesian network model based on knowledge of mycological experts to depict habitat attributes that predict presence of the rare polypore *Bridgeoporus nobilissimus*. The probabilities in the working model were then adjusted with field survey data of presence or absence of the polypore, thereby improving the model's predictability. The model was used to find additional sites in the planning area and also alerted managers to key habitat elements (in this case large boles of *Abies procera*) to maintain on the landscape. Lesher (2005) used a different approach to model suitable habitat for the rare SMSCP lichen *Hypogymnia duplicata* by combining ecoclimatic regional data that maps potential vegetation (Henderson 2001) with stand-scale habitat data taken from known sites of the lichen. She validated the model by conducting surveys in predicted locations and found many new locations. A map of the lichen's potential suitable habitat showed that the habitat was well distributed in reserves, thus allowing the lichen's removal from the protected species list. This approach could also be used to model fungus distribution.

Habitat modeling uses many other analytical approaches depending on objectives and scale, and there are excellent examples of fungal habitat models for individual species such as chanterelles (Trappe 2004b; Kranabetter *et al.* 2009) and lobster mushrooms (Rochon *et al.* 2009), guilds and species of hypogeous fungi in Australia (Claridge *et al.* 2000a, b, 2009b; Jumpponen *et al.* 2004), production of wild, edible mushrooms in Spain (Bonet *et al.* 2010), and habitat preferences for Red-listed fungi in Sweden (Berg *et al.* 2002).

Habitat modeling provides three potential benefits for fungus conservation. First, it helps to systematically organize our thinking about key resource and environmental attributes that contribute to fungal presence and successful reproduction. Second, models are in essence hypothesis generators that provide assumptions testable through surveys and research and thereby improve our understanding of habitat. And third, models can help to identify critical habitat attributes that managers can consider for protection or restoration during the planning process. Protection is more important than attempts to restore habitat, because no disturbed habitat is truly restored, it is just modified in an attempt to imitate what we suppose the original habitat was. No data are available on restoration success for rare fungi, but common and adaptable fungi such as *Rhizopogon* spp. do reappear in clearcuts after the following plantations have reached a stage of development in which *Rhizopogon* can fruit.

Applying ecological knowledge and the power of molecular tools

Mycology has accumulated incredible amounts of ecological knowledge over the last 15 yr through use of powerful molecular DNA tools. Although much of the molecular research effort has been directed towards systematics and evolutionary biology of fungi, from the outset researchers have also applied molecular tools towards ecological questions (Horton & Bruns 2001). But are we asking ecological questions and collecting data useful for addressing conservation information needs noted previously? Ecological research currently aims towards better understanding of fungal diversity in various ecosystems, community composition and function, and response to disturbance. All these relate to fungus conservation but could be enhanced by addressing conservation objectives in field study designs. For example, we might consider integrating micro- and macrohabitat characteristics in community studies, analyzing biodiversity data to identify indicator species of composition or function, and examining response of fungi to changing environments at various spatial and temporal scales. Given the attraction and power of molecular approaches in fungal ecology, it is crucial that mycologists consider how those approaches also can be focused on conservation information needs.

Molecular tools provide unprecedented ability to investigate fungal ecology, in part because fungi can now be identified from their vegetative structures. This overcomes issues encountered with sporocarp surveys, but molecular approaches also have limitations. For instance, while sporocarp surveys can cover large spatial areas (tens of square meters), belowground sampling typically covers only a small fraction of a plot (single soil samples often cover only several square cm of forest floor). The problem of sampling vegetative structures is exacerbated by the fine-scale patchiness of fungi below ground. Still, we have learned a great deal with these approaches. Because of the high number of species that occur in only one or two samples, estimates of species richness are typically much higher than the observed species richness. Further, a species effort curve rarely reaches the asymptote, suggesting that with additional sampling, estimates of richness will increase. If it was not apparent before, molecular tools have revealed that fungal diversity is typically incredibly high.

A related question key to fungus conservation is whether high species diversity translates into high functional diversity or if many species share similar functions. Molecular tools now allow us to unravel those functional questions in field settings and provide insight into other conservation issues such as defining individuals and determining population structure and dispersal strategies as exemplified below.

Examining the response of EM fungi to atmospheric nitrogen deposition

The following example shows how observed patterns of reduced species richness based on sporocarp records prompted research to elucidate the mechanisms behind the loss in diversity. Arnolds (1991) reported a pattern of reduced species richness of EM fungi strongly correlated with anthropogenic nitrogen (N) pollution. To investigate the belowground response to elevated N availability, investigators have since used manipulation experiments with N additions or existing anthropogenic gradients of N deposition and molecular tools to identify EM fungi on root tips (Peter *et al.* 2001; Lilleskov *et al.* 2002; Avis *et al.* 2003). These studies found that whereas sporocarp production and presence of some species were reduced, several other species persisted as ectomycorrhizas on sampled root tips, evidence of a delayed response in the vegetative structures. Although not all EM fungi respond identically, the general trend is a reduction of species richness in EM fungi with increased N availability.

These results led J. Vineis & T. Horton (personal communication) to hypothesize that fewer EM fungal species should be observed at the high end of a natural N availability gradient than at the low end. However, they found no difference in the species richness along a natural N availability gradient in the White Mountains of New Hampshire, although the assemblage of species changed (J. Vineis & T. Horton, unpublished data). It is possible that the loss in species richness observed in earlier studies is a response to disturbance of rapid N availability rather than N availability *per se*. However, one group of EM fungi is significantly reduced in high N availability plots regardless of whether the source of N is anthropogenic or not, the so-called medium-fringe exploration types such as *Cortinarius* and *Piloderma* (see Agerer 2001 for a review of the exploration types).

Recent work by Hobbie & Agerer (2010) suggests that many medium-fringe to long-distance exploration types have unique enzymatic capacities for accessing organic N sources (see Lilleskov *et al.* 2010). Although preliminary, they suspect that the fungal species hardest hit under elevated levels of inorganic N from anthropogenic sources are those capable of accessing organic N. Importantly, the species that are negatively impacted by N pollution produce large amounts of hyphae in soils and thus forests may lose an important carbon sink with the loss of these species. *Russula* and *Lactarius* were equally abundant along the natural N availability gradient (J. Vineis, unpublished data) and have been shown to fruit more abundantly with N addition (Avis *et al.* 2003). Species of *Russula* and *Lactarius* produce sparse hyphae away from the root (so-called contact exploration types, Agerer 2001) and appear to be less capable of accessing organic N. It is possible that the contact exploration types rely more on ammonium and nitrate, the N sources found in polluted areas and used in manipulation studies. By using molecular tools and isotope analyses we have learned about the functional roles of some of these fungi with respect to N cycling in the field, gained insights into mechanisms leading to species responses under N pollution, and identified a group of fungi that may be vulnerable to local extirpation in areas with high N deposition.

Defining individuals and determining population structure

Determining rarity and understanding conservation status for a species are often based on knowledge of the number of individuals and its population structure. Without molecular tools, it is virtually impossible to know how many individuals are represented when multiple sporocarps of a species appear in a forest; are they all from one individual or do they represent multiple individuals? Smith *et al.* (1992) were among the first to employ molecular tools to address this question; they reported that an individual of *Armillaria gallica* was among the largest (15 ha) and longer-lived (1 500 years old) organisms on Earth. While it is true that individuals of culturable species such as *A. gallica* can be subjected to somatic incompatibility tests, this approach may not be as effective at identifying individuals as molecular approaches (Jacobson *et al.* 1993). Given that many EM fungi cannot be isolated and grown in culture, molecular tools have been especially important for determining individuals – and thus population size – of EM fungi.

We now have considerable evidence, initially from somatic incompatibility or, more lately, from molecular studies, that different EM fungal species vary in their spatial extent and temporal persistence. Species of *Suillus* and *Rhizopogon* can be quite large, covering tens of m^2 (Dahlberg & Stenlid 1990; Bonello *et al.* 1998; Kretzer *et al.* 2005). If the vegetative portion of the individual covers a large spatial area, it can be assumed, based on extension rates, that the individual is a long-lived perennial, spreading through the soil over time. Individuals of *Amanita*, *Cantharellus*, *Laccaria*, *Lactarius*, *Russula*, and *Tricholoma* are typically smaller (Gherbi *et al.* 1999; Redecker *et al.* 2001; Bergemann & Miller 2002; Dunham *et al.* 2003; Gryta *et al.* 2006), and probably shorter-lived than *Suillus* and *Rhizopogon*. For those that reproduce annually and are short-lived, a reduction in sporocarp production may be particularly worrisome from a conservation perspective if the population is small and isolated.

Estimating the size of fungal individuals is also important because it provides knowledge about the mode of dispersal and population viability. For instance, Dunham *et al.* (2003) observed a predominance of small genets that were less than 4 m in diameter for *Cantharellus formosus* and suggested that genet propagation was primarily a result of basidiospore dispersal rather than vegetative spread. Kretzer *et al.* (2005) reported that *Rhizopogon vesiculosus* was more strongly clustered than the sympatric species *Rhizopogon vinicolor*, and that vegetative spread and genetic differentiation was more important for *R. vesiculosus* than *R. vinicolor*. Kretzer *et al.* (2005) also did a parentage analysis and found eleven possible pairs in the two species but only two of the *R. vinicolor* pairs were supported as parent/offspring as opposed to siblings. The

Table 1 – Principles and considerations for conservation and management of ectomycorrhizal fungi in temperate forests[a]

Principle	Justification	Management considerations
Maintain habitat diversity at landscape scales	Fungal species have evolved within a shifting mosaic of forest age classes, plant community dynamics, and periodic disturbances across broad landscapes over millennia.	• Protect and restore old-growth forests because this habitat has diminished significantly due to forest harvest • Maintain a diversity of forest successional age classes across the landscape • Pattern these elements on the landscape to provide for fungal dispersal and population establishment
Maintain habitat diversity at forest stand scales	Fungal species often reside in unique niches and respond to myriad microhabitat conditions.	• Maintain or develop habitat diversity within the forest stand to provide ample latitude for fungi to establish and reproduce • Attributes to consider include plant composition, organic matter, coarse wood, openings, and soil quality
Maintain host diversity	Many ectomycorrhizal and saprobic fungi associate with specific host plants and others with a diverse array of hosts.	• Avoid tree monocultures by planting a diversity of native trees in mixtures that resemble natural assemblages • Diversify the understory vegetation; shrubs and herbs act as hosts or create unique microhabitat
Maintain soil health	Most soil fungi are aerobic and consume diverse organic and mineral resources.	• Avoid soil compaction and hot surface fires that destroy soil structure, particularly the stable aggregates that allow for air and water movement • Avoid removal of the litter layer and minimize disturbance to the forest floor • Maintain natural levels of soil organic matter
Maintain legacy trees and limit size of timber harvest units	Some trees typically survive historical natural disturbances such as fire, and maintain fungal populations on live roots. When all tree hosts are removed (e.g., clearcuts), fungal populations are reduced and slow to recover compared to forest thinnings or partial cuts.	• Retain legacy trees (green tree retention) in cutting units to maintain live fungal populations on roots • Avoid large clearcuts • Consider various thinning approaches or aggregating uncut trees to create reservoirs of fungal diversity and allow for fungal dispersal into disturbed areas • Maintain refuge understory plants that may act as mycorrhizal hosts or create microhabitat within the future forest stand • Plant seedlings soon after harvest before residual fungal inoculum in the soil diminishes
Protect known locations of rare fungi and fungal diversity hotspots	Repeated collection and inventory of fungi in several regions worldwide have documented locations for rare species or areas where fungal richness remains high such as in parks or reserves.	• Protect known sites of rare species by minimizing disturbance and maintaining critical habitat elements • Identify fungal diversity hotspots and work with responsible public and resource managers to protect these areas or designate them as fungal reserves
Monitor fungal populations	Several years of data collection are needed to detect trends in population stability for rare species or fungal communities.	• Establish permanent monitoring locations for targeted species or fungal communities • Include fungal monitoring within long-term biodiversity monitoring programs • Include volunteer citizen scientists in the design and implementation of fungal monitoring programs

Table 1 (*continued*)

Principle	Justification	Management considerations
Develop partnerships with the public, other scientists and resource managers	Species conservation is a complex process and expensive undertaking. Mycologists cannot do it alone and should take advantage of other on-going biodiversity monitoring and conservation programs.	• Promote fungal workshops and field trips to educate the public and resource managers as to the importance of fungi in ecosystems and principles for their conservation • Seek opportunities to integrate fungal conservation goals within other on-going multi-taxa conservation programs • Work directly with resource managers to include fungi in various adaptive management or research programs

a Consolidated and modified from management strategies presented by Wiensczyk et al. (2002) and Trappe et al. (2009a). Many of the principles overlap. Although most of these principles and considerations were developed for ectomycorrhizal fungi, they have relevance to all forest fungi, and serve as examples for how guidelines can be developed for fungi in general.

distances between the parents and offspring indicated spore dispersal was of the order of tens of meters. Grubisha et al. (2007) found populations of *Rhizopogon occidentalis* and *Rhizopogon vulgaris* were highly structured over distances of less than 9 km with significant isolation by distance, a result of spore dispersal limitations between disjunct host patches and geographic barriers. These two *Rhizopogon* studies suggest that population dynamics can vary within a genus, a pattern also observed in *Tricholoma* (Gryta et al. 2006; Lian et al. 2006). Gryta et al. (2006) found that *Tricholoma populinum* spread by vegetative growth while *Tricholoma scalpturatum* spread through sexual spore dispersal. We need additional data for many EM fungal groups, including information on distance and mode of dispersal, so it is important not to generalize about population dynamics even within a genus. The population studies above illustrate the power that molecular tools can bring to understanding fungal population dynamics and will be of immense value in fungus conservation if mycologists target their use to address conservation information needs.

Are ectomycorrhizal fungi everywhere? Getting a handle on fungal dispersal

The Baas-Becking hypothesis on the distributions of microorganisms states: (1) that everything is everywhere, and (2) the environment selects (Baas-Becking 1934). While long-distance dispersal of spores for some fungi is impressive (Moncalvo & Buchanan 2008), it is increasingly evident that dispersal capacities of EM fungi are limited, so their spores are not ubiquitous. For instance, combining field data and mathematical models, Galante (2009) reported that 95 % of the spores fall less than 50 cm from the cap of origin for six epigeous, and presumably wind-dispersed, EM fungi. It is possible that the estimated 5 % of the spores that disperse further than 50 cm may support the establishment of new individuals after long-distance dispersal. But when spores are dispersed by wind, they become increasingly diffuse with distance from the source and there is good evidence that the spores of most species do not remain viable long enough to accumulate as a spore bank (reviewed in Nara 2008), reinforcing the local scale pattern around established individuals and the sporocarps they produce.

Additional evidence that everything is not everywhere comes from locations where Pinaceae have been introduced. Repeated attempts to establish pine plantations in the southern hemisphere failed until seedlings preinoculated with mycorrhizal fungi were planted (Young 1940; Vozzo & Hacskaylo 1971; Mikola 1990; Read 1998). Nuñez et al. (2009) reported that species of Pinaceae that are invasive in many locations are prevented from establishing away from plantations on Isla Victoria, Argentina, because of a lack of compatible EM fungus inoculum in native soils. Although compatible inoculum is found close to the plantations where seedlings are establishing, dispersal limitation of the fungi reduces inoculum in soils at increasing distance from the plantations, inhibiting seedling establishment and subsequent invasion.

These studies highlight that for most EM fungi, long-distance dispersal is more limited than previously thought. However, the lack of genetic structure among subpopulations of some fungal species in continuous forests (Zhou et al. 2001; Bergemann et al. 2006; Pitcher 2009) suggests that relatively long-distance dispersal of meiotic spores, and subsequent establishment of new dikaryons, between isolated subpopulations does occur. If forests become so fragmented to prevent such dispersal and establishment, then the subpopulations may become too isolated and go locally extinct. Unfortunately, our knowledge about population dynamics of these fungi is still relatively rudimentary and developing reliable management recommendations based on these findings is difficult at this time.

Running fast just to keep up with advances in molecular methods

Given the rise of molecular methods, several recent reviews highlight how fungal ecology is advancing at an impressive rate (Peay et al. 2008; Hibbett et al. 2009; Comas et al. 2010; Parrent et al. 2010). The pace of advancement will likely continue because new molecular techniques are rapidly evolving. For example, high throughput sequencing now enables fungal ecologists to saturate species effort curves, in part because 454 sequencing allows rapid generation of tens of thousands of sequences (Buée et al. 2009; Jumpponen & Jones 2009; Öpik et al. 2009). With such output, however, bioinformatics becomes a major challenge; how does one analyze these numerous sequences and apply them in a meaningful way to advance our knowledge of fungal ecology and conservation?

Shortcomings of information in GenBank also create difficulties in applying molecular analyses. For instance, many sequences deposited in GenBank and other public databases lack taxonomic information. Brock *et al.* (2009) submitted ITS sequences from sporocarps housed in a herbarium collection to BLAST searches in GenBank and found about 10 % had high similarity to sequences labeled as unknown environmental samples. Another 70 % of the sequences in the Brock *et al.* (2009) study were not represented in GenBank at all, highlighting that herbarium collections are an under utilized source of taxonomic information. Ryberg *et al.* (2008) found many unidentified ITS sequences in GenBank were *Inocybe* species based on sequence similarity to voucher collections. Although there are good reasons to conservatively apply names to sequences from environmental samples, in most cases, some taxonomic information can be attached. For example, one might notice clamp connections in the fungal mantle of an EM root tip and use this to identify the fungus as a Basidiomycete. Researchers can now do a BLAST search in GenBank that filters out all unidentified sequences, but one wonders what potential matches are lost due to lack of taxonomic information.

Further problems in using GenBank arise from the many sequences that are full of errors or have the wrong name applied and all too often are not represented by voucher collections accessioned into a public herbarium (Vilgalys 2003; Trappe 2004a; Nilsson *et al.* 2006; Bidartondo 2008), and third party annotations are still prohibited. The Fungal Environmental Sampling and Informatics Network (FESIN, Bruns *et al.* 2008) and the User-Friendly Nordic ITS Ectomycorrhiza Database (UNITE, Koljalg *et al.* 2005) are addressing these problems with projects to house sequences from named voucher specimens that have been vetted by taxonomic experts and will allow third party annotations (Horton *et al.* 2008; Peay *et al.* 2008). GenBank has proven extremely valuable as a diagnostic tool for identifying DNA from environmental samples (e.g., root tips, soil, etc.). But the swell of misidentified and unidentified sequences in the database has become a major problem; the fixes listed above will help.

Two major advances in molecular tools may prove valuable for fungal ecology and conservation: linking the phylogenetic signal from DNA sequences to functional traits (Cavender-Bares *et al.* 2009; Parrent *et al.* 2010) and sequencing entire genomes of target fungi. Tools such as Phylocom (Webb *et al.* 2008) and UniFrac (Lozupone *et al.* 2006) are now being applied in ecological studies with impressive results (Powell *et al.* 2009; McGuire *et al.* 2010). Genome sequences constructed for a number of fungal species provide insights into the biology of the fungi. For instance, the *Laccaria bicolor* genome project has led to insights into the mycorrhizal symbiosis (Martin *et al.* 2008) and the *Amanita bisporigera* genome project has yielded insights into the genes involved in toxin production (Hallen *et al.* 2007). These advances are leading mycologists into another new, exciting phase of research that will offer conservation biologists unprecedented levels of understanding about fungi in forest communities.

Adaptive management and management guidelines

Protecting species at risk is not a static process because species populations, habitats, and management objectives and activities change through time (Olson 2007). Thus, we cannot expect to design a particular conservation approach, e.g., designate a reserve, and walk away believing we have accomplished our conservation objective. The high degree of uncertainty surrounding the conservation of rare or little-known fungus species suggests that mycologists help design conservation approaches as testable management hypotheses. Olson (2007) and Dahlberg *et al.* (2009) emphasize use of adaptive management for conserving rare or little-known species. Adaptive management is in essence a cyclic learning process that begins with an assumption or hypothesis of the best management approach given current knowledge. That hypothesis is tested by designing and implementing the preferred approach on the ground; the test concludes its first iteration with collection of additional information (monitoring) as established in the design to examine how well conservation objectives were met. Once the new information is analyzed and evaluated (and even integrated into updated species-habitat models), the approach is modified as needed and a new round of monitoring is conducted. The approach is designed with learning objectives and periodic monitoring so continual improvements can be made.

The SMSCP used an adaptive approach by protecting individual species sites along with reserves and structural elements (e.g., large woody debris) of old-growth forests, and then collecting information through plan-wide regional surveys (Molina *et al.* 2003). Over time, new data showed that many species were indeed rare (they continued to receive conservation protection), while others were not rare or were adequately protected within reserves and removed from the species-specific protection list. Key to success of the program was regularly scheduled monitoring to test the original assumptions of the design. As noted for harnessing expert knowledge, designing adaptive management approaches for fungi may work best when done in cooperation with resource managers, particularly when fungus conservation objectives are integrated into a comprehensive management plan.

Until mycologists design and test specific approaches for conserving fungi at various scales, they can provide general guidelines to resource managers and the public on how to appreciate and protect fungi. Wiensczyk *et al.* (2002) and Trappe *et al.* (2009a) provided several examples of conservation principles, guidelines, and strategies for ectomycorrhizal fungi (Table 1) in forests of western North America; most of these guidelines derived from knowledge of fungal biodiversity and ecology, and effects of forest management practices and natural disturbance on fungal communities. They ranged from protecting individual sites for rare species or fungal diversity hotspots, to delineating critical habitat for protection at stand and landscape scales.

The assumptions behind these management guidelines can be tested in new research studies as part of an applied adaptive management program, thus improving the guidelines. For example, studies could determine the optimum tree species mix and tree density to promote fungal diversity in a targeted forest ecosystem. Similarly, studies also could determine quantity and quality of coarse woody debris to benefit fungal communities. Such studies will continue to build the scientific foundation for sharpening our understanding of how best to protect and restore key habitat elements, and thus to advance fungus conservation.

Conclusions

Fungus conservation is complex and challenging due to high species diversity, a large number of rare or little-known species, poor understanding of habitat requirements, and high uncertainty about how to conserve species in natural and disturbed landscapes. However, dealing with uncertainty is part of the scientific method, so mycologists should not let this challenge daunt them into inaction. The collective knowledge of mycologists based on decades of careful field observation is considerable and can be formally compiled and applied to conservation issues through thoughtful organization, summary, and publication of personal databases, observations and models. Working directly with resource managers in the planning process often is the most effective way to put personal knowledge into practice, but documentation and distribution of that knowledge also are paramount.

Conservation biology has developed into a discrete scientific discipline over the last few decades. As relative newcomers, mycologists should take advantage of the many options and approaches developed by the conservation and management community for other taxa. In addition to protecting species through Red-listing analyses, it is particularly important that mycologists also examine coarse-scale, system approaches that may provide general protection for large assemblages of fungi, including rare, common, and little-known species alike. Use of systems approaches and broad-scale management schemes requires an enhanced understanding of habitat associations of fungi in space and time. Thus, we emphasize that mycological societies develop generalized frameworks for defining fungal habitat including key biological and environmental attributes; new research also should consider development of habitat models for representative fungi that support habitat restoration and management.

Gaining information and closing the gap on uncertainty, however, require that we integrate development and testing of conservation guidelines into our on-going fungal ecology research programs. Harnessing the power of molecular tools to address questions regarding the presence, persistence and dispersal of individuals, and population structure at different spatial scales, will be especially valuable to fungus conservation science. Finally, although we will never have complete knowledge of fungal biology and ecology to guide conservation, this situation is not unique to fungi. We currently have enough knowledge to make scientifically sound management recommendations and to develop strategies to integrate fungi into conservation programs and resources management activities. Proposed conservation strategies can be steadily improved by embracing adaptive management principles wherein we test hypothesis-driven conservation methods, monitor results for effectiveness, and incrementally enhance strategies by applying what we have learned.

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