Conservation Biology

Essay

A fungal perspective on conservation biology

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Abstract: *Hitherto fungi have rarely been considered in conservation biology, but this is changing as the field moves from addressing single species issues to an integrative ecosystem-based approach. The current emphasis on biodiversity as a provider of ecosystem services throws the spotlight on the vast diversity of fungi, their crucial roles in terrestrial ecosystems, and the benefits of considering fungi in concert with animals and plants. We reviewed the role of fungi in ecosystems and composed an overview of the current state of conservation of fungi. There are 5 areas in which fungi can be readily integrated into conservation: as providers of habitats and processes important for other organisms; as indicators of desired or undesired trends in ecosystem functioning; as indicators of habitats of conservation value; as providers of powerful links between human societies and the natural world because of their value as food, medicine, and biotechnological tools; and as sources of novel tools and approaches for conservation of megadiverse organism groups. We hope conservation professionals will value the potential of fungi, engage mycologists in their work, and appreciate the crucial role of fungi in nature.*

Keywords: decomposers, ecosystem services, forest ecology, indicator species, lichens, mycorrhizal fungi, non-timber forest products, pathogens

Una Perspectiva Micótica de la Biología de la Conservación

Resumen: *Hasta el momento, los hongos rara vez han sido considerados dentro de la Biología de la Conservación, pero esto está cambiando conforme la disciplina cambia su enfoque en problemas de especies individuales hacia una estrategia integrada basada en los ecosistemas. El énfasis actual en la biodiversidad como proveedor de servicios ambientales enfoca la atención en la amplia diversidad de hongos, sus papeles cruciales en los ecosistemas terrestres y los beneficios de considerar a los hongos en sintonía con las plantas y los animales. Revisamos el papel de los hongos en los ecosistemas y elaboramos un resumen del estado actual de su conservación. Hay cinco áreas en las cuales los hongos pueden integrarse inmediatamente en la conservación: como proveedores de hábitats y procesos importantes para otros organismos; como indicadores de tendencias deseadas o indeseadas en el funcionamiento del ecosistema; como indicadores de hábitats con valor de conservación; como proveedores de enlaces fuertes entre las sociedades humanas y el mundo natural debido a sus valores como alimento, medicinas y herramientas biotecnológicas; y como una fuente de*

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herramientas y estrategias novedosas para la conservación de grupos megadiversos de organismos. Esperamos que los profesionales de la conservación valoren el potencial de los hongos, integren a los micólogos en su trabajo y aprecien el papel crucial de los hongos en la naturaleza.

Palabras Clave: descomponedores, ecología de bosques, especies indicadoras, hongos micorrízicos, líquenes, patógenos, productos no-maderos de los bosques, servicios ambientales

Introduction

Since the Rio Convention on Biological Diversity was signed in 1992, the conservation of biological diversity has been an important topic in international politics, and the urgent need for action was reignited at the tenth meeting of the Conference of the Parties to the Convention on Biological Diversity in Nagoya (CBD 2010). Conservation initiatives have evolved since the late 20th century from an initial focus on protection of pristine areas and particular (charismatic) species of animals and plants to a more holistic ecosystem-based approach (e.g., Salafsky et al. 2002). So far fungi have received limited emphasis in conservation biology (Griffith 2012), except as potential threats to ecosystems, individual species, or species groups (Fisher et al. 2012). Reasons for this neglect are complex but seem related to a general suspicion of fungi in the English-speaking world, their hidden lifestyle and challenging diversity, and a historical classification as an odd division of the *Plantae* (Minter 2010). We are certain the situation is changing due to an ongoing revolution in methods to obtain data on fungal species and communities and because fungi are the foundation of a variety of ecosystem services.

We sought to indicate directions toward a full and balanced appreciation of fungi in conservation biology. We reviewed the critical roles fungi play in ecosystems and provide an overview of the current state of fungal conservation. We found that fungal conservation is important in its own right and stress that consideration of the fungal component of biodiversity can benefit conservation in general.

Fungi as Ecosystem Actors

Fungi constitute a megadiverse kingdom. There are at least 1.5 million, but probably as many as 3–5 million species, of which only about 100,000 have been described formally (Blackwell 2011; Scheffers et al. 2012). Some are unicellular, but the majority form mycelia, which range in size from a few millimeters to some of the largest organisms on the planet; for example, honey fungi [*Armillaria* spp.] mycelia can occupy many hectares of forest floor. Most fungi are hidden in the substrates they inhabit. Some form fruit bodies periodically or cause visible symptoms in host plants, but only lichens are generally visible throughout most of their lifecycle. Dispersal is usually passive and maintained by microscopic windborne spores, but aquatic dispersal and animal vectors are important for many species. Profuse spore production may easily lead to the view that fungi generally have much wider distribution ranges and face less dispersal limitation than most other multicellular organisms. But this is probably not the case; recent research on spore dispersal (e.g., Norros et al. 2012; Peay et al. 2012) and fungal biogeography (Taylor et al. 2006; Salgado-Salazar et al. 2013) shows that fungi tend to be less well dispersed and ubiquitous than believed.

Fungi maintain crucial processes in terrestrial ecosystems as decomposers of dead plant tissues and mutualistic partners of almost all terrestrial multicellular organisms. Decomposer fungi are especially prominent in forests and other ecosystems where grazing, fire, or human harvest of plant material is not dominant in carbon cycling (Boddy et al. 2008). Plants produce between 5 and 33 t/ha of organic matter in forest ecosystems every year, and an estimated global carbon pool of 73 petagrams is bound in dead wood (Pan et al. 2011). Most of this organic matter is lignocellulose, a complex of recalcitrant biopolymers that only fungi can decompose efficiently (Boddy et al. 2008). Fungal decomposition is crucial for the release of nutrients and energy stored in plant litter, so fungi form the basis of soil food chains and are grazed on directly or indirectly by a wide range of invertebrate and vertebrate taxa (Stokland et al. 2012).

Fungi are involved in diverse mutualistic associations. Lichenized fungi associated with green algae or cyanobacteria are highly stress tolerant and mediate most primary production and nitrogen fixation in desert and polar ecosystems, which cover 6% of the World's surface (Shaver & Chapin 1991). In other climate zones, they dominate microhabitats such as tree trunks, rock surfaces, and living leaves of rainforest trees (Scheidegger & Werth 2009). Most plants (approximately 90% of species) rely on mycelial networks intimately connected with their roots, mycorrhizas, for the uptake of water and N, P, and other minerals from soil. In return, mycorrhizal fungi receive substantial amounts of sugars from their plant partners, typically 15–30% of the net primary production (Smith & Read 2008).

Mycorhizal fungi are not only important for nutrient cycling, but also for mineral weathering and carbon storage in forest ecosystems (Courty et al. 2010; Clemmensen et al. 2013). Further, they are intimately involved in plant competition, and because different groups of fungi have very different enzymatic capacities, changes in plant composition mediated by natural or anthropogenic processes might result in dramatic shifts in ecosystem processes (Averill et al. 2014).

More cryptically, the internal tissues of all vascular plants host diverse communities of fungal endophytes, of which some are mutualistic and prevent attacks from pathogens and herbivores, whereas others are decomposers with a latent invasion strategy (e.g., Rodriguez et al. 2009). Fungal endophytes represent a hyperdiverse group globally, both in terms of unknown species and undiscovered bioactive compounds (Arnold & Lutzoni 2007; Smith et al. 2008). As a functional group, they are not clearly delimited from fungi classified as pathogens. In some cases, beneficial fungi may become pathogenic due to environmental changes or an imbalance in coevolutionary processes. For example, the recent outbreaks of ash dieback in Europe are caused by the endophytic *Hymenoscyphus pseudoalbidus* (syn.: *Chalara fraxinea*), which originates in Eastern Asia where it lives in non-pathogenic association with Manchurian ash (*Fraxinus mandschurica*) (Zhao et al. 2012; Pautasso et al. 2013).

The public perception, and perhaps that of many conservation biologists, is that fungi are extremely harmful because of the pathogenic nature of a few species (Fisher et al. 2012). Well-known examples include the apparent extinction of more than 60 amphibian species due to chytridiomycosis (Pounds et al. 2006) and the alteration of European and North American landscapes by chestnut blight, Dutch elm disease, and ash dieback (Loo 2009; Pautasso et al. 2013). However, natural disturbances are integral to the functioning and continued evolution of ecosystems, and recent studies suggest pathogenic fungi are drivers of biodiversity in tropical forest ecosystem due to their density dependent attacks on species that might otherwise become dominant by competitive exclusion (Bagchi et al. 2014). Many outbreaks of pathogenic fungi are caused or strongly reinforced by human actions, not least the unintentional movement of fungal species around the globe (e.g., Brasier 2008).

Current State of Fungal Conservation

Threats to fungi are essentially the same as threats to animals and plants, including the degradation, loss, and fragmentation of natural habitats, climate change, and deposition of nitrogen and other pollutants (Sala et al. 2000; Dahlberg et al. 2010).

Fungal conservation is most highly developed in Fennoscandia (Dahlberg et al. 2010), a region of relatively low overall biodiversity. Government finances the production of red lists of animals, plants, and fungi, and these groups have equal priority for conservation. This integrative approach has fueled fungal conservation for three reasons. First, fungi in Fennoscandia constitute a significant part of the total biodiversity because the boreal zone consists largely of coniferous forests, which provide a wealth of niches for fungi but host relatively few vascular plants and larger animals. Second, Fennoscandia has a long tradition in fungal taxonomy and a large and knowledgeable community of amateur field biologists, which have resulted in an increasing knowledge of the ecology and rich data on the distribution of macrofungi. Third, as a consequence of the countries' conservation goals encompassing all groups of organisms, the focus of conservation is directed more toward habitats than specific species. In practice, species from many groups are considered together to identify and prioritize conservation measures, and fungi are well suited as indicator species to identify sites, in particular forests, with specific conditions and histories.

Fungal red lists are now widely used for management and conservation activities across Europe; 33 of the 35 national red lists of fungi are for European countries and 2 have been produced for other parts of the world (New Zealand and Japan) (Dahlberg & Mueller 2011). A few countries, including Finland, Norway, Sweden and the United Kingdom, have launched action plans to protect specific fungal habitats and species, and in at least 12 European countries there are examples of fungi being considered in selection and prioritization of nature reserves (Dahlberg et al. 2010). Outside of Europe and the Pacific Northwest region of the United States (Molina 2008), initiatives and strategies to conserve fungal biodiversity are more scattered (but see Buchanan & May 2003; Manoharachary et al. 2005; Abdel-Azeem 2010); only three fungal species are currently globally red listed. However, the situation is changing. The International Union for Conservation of Nature (IUCN) aims to have several hundred fungal species on their red list in the near future (IUCN 2013). Organizations dedicated to fungal conservation are also on the rise. The European Council for the Conservation of Fungi (ECCF) was formed in 1985, and in 1991 a fungal specialist group was established within the IUCN. Since 2007, fungal conservation groups have also been established in Africa, South America, and the United States (Barron 2011), and an International Society for Fungal Conservation (ISFC) was founded in 2011, suggesting a need for attention to fungal conservation at both the national and international levels.

Benefits of Including Fungi in Conservation

Many conservation professionals acknowledge that human well-being and social resilience depend on global biodiversity, a view that is formalized in the concept of ecosystem services. The Millennium Ecosystem Assessment (World Resources Institute 2005) grouped ecosystem services into four categories—regulating, supporting, provisioning, and cultural services. Like other multicellular organisms, fungi provide all of these services (Pringle et al. 2011), but the fundamental role fungi have as regulators of ecosystem processes in terrestrial ecosystems makes them central to sustainable land use (Parker 2010; Mace et al. 2012). However, it is just as evident that the majority of threatened fungi do not contribute ecologically to, and cannot even survive in, areas managed for timber and crop production. We believe fungi deserve conservation in their own right, but below we review how conservation in general can benefit from the inclusion of fungi.

Fungi Providing Services for Other Organisms

Most of the key processes driven by fungi (e.g., recycling of nutrients from dead wood and maintenance of plant nutrition by mycorrhizal fungi) derive from the combined action of larger ecological guilds (Fig. 1a). Within guilds fungal communities are often very species rich, which suggests high levels of functional redundancy. Both experimental (e.g., Strickland et al. 2009; Fukami et al. 2010) and explorative studies (e.g., Taylor et al. 2014) report high levels of niche differentiation and less redundancy than expected in fungal communities, indicating that species identities matter in major ecosystem processes where fungi contribute.

Fungi provide a direct principal food resource for many organisms, including mammals, orchids, and insects. Polypores and other long-lived fleshy fruit bodies are particular rich habitats for dependent insects, especially beetles and diptera. For example, the dryad's saddle (*Polyporus squamosus*) hosts over 246 beetle species in Europe (Benick 1952). Other fungi are involved in the formation of microhabitats, such as cavities in trees, that are critical for some birds, mammals, arthropods, and epiphytes (Fritz & Heilmann-Clausen 2010; Remm & Lõhmus 2011; Cockle et al. 2012). In many cases, associations are species specific or selective, implying that understanding of the fungal part of the association is crucial for the conservation of the dependent species, as has been described for rare beetles associated with bracket fungi (Komonen 2003), orchids dependent on specific suites of mycorrhizal partners (Batty et al. 2002), and threatened marsupials dependent on truffles for food (Claridge & May 1994).

Fungi as Indicators of Ecosystem Processes

The narrow and thin-walled hyphae of fungi are exposed to chemicals in the environment and are highly sensitive to microclimatic gradients. Lichens are among the most sensitive organisms regarding air quality. In fact, the earliest record of biodiversity loss resulting from human industrial activity was made by Thomas Pennant in 1773, who observed the decline of lichens as a result of copper smelting at Parys Mountain, Wales (Pennant 1781). The differential sensitivities of lichens to SO_2 and other airborne pollutants have since been widely used as a proxy measure of air quality in both urban and natural areas (Nimis et al. 2002).

Non-lichenized fungi are also affected by SO_2 pollution, but anthropogenic nitrogen pollution is now the most pervasive threat. The decline of some mycorrhizal species (e.g., stipitate hydnoids and *Cortinarius* spp.) have been particularly dramatic, though more widespread changes in species composition in polluted areas are of equal concern (Arnolds 2001; Lilleskov et al. 2011).

The effects of global climate change on fungi are difficult to quantify, but it is apparent that climate warming over recent decades has altered the phenology of fungal fruiting. For example, many fungi previously known to fruit only in the fall now also fruit in spring (Kauserud et al. 2012). Changes in fungal community structure provide an early warning of changing ecosystem processes, but so far there have been few efforts to implement this in standardized monitoring schemes. Broadly, fungi constitute the most visible link to the vast biodiversity underground and are basal to the highly diverse decomposer food chains. Incorporating fungi into ecosystem level indices such as the biodiversity intactness index (Scholes & Biggs 2005) and the living planet index (Loh et al. 2005), which so far neglected decomposers in general, would greatly enhance the value of these indices.

Fungi as Indicators in Conservation Planning

The very specific habitat requirements of fungi make them well suited as indicators for selecting conservation areas and monitoring their status. Accounting for fungi in an area expands understanding of the biotic space and emphasizes microhabitats and processes that are pivotal for biodiversity but easily overlooked if fungi are not considered. For instance, specialized wood-inhabiting fungi may be absent from otherwise valuable woodland areas due to the lack of old trees and dead wood, and may be extirpated in a landscape if remaining old-growth areas are fragmented (Stokland et al. 2012). Similarly, some mycorrhizal and lichenized fungi are highly sensitive to breaks in forest continuity and may be lost from forest ecosystems if mature trees are not retained through rotations (Coppins & Coppins 2002; Rosenvald & Lõhmus 2008). These processes are also important for many other organisms, including arthropods, mollusks, and microfauna; in practice fungi are often the easiest group to monitor.

Especially in Europe, several indicator schemes based on fungi have been suggested to assess the conservation value of forests and grasslands (Heilmann-Clausen & Vesterholt 2008) (Fig. 1b), and in Sweden and the Baltic countries fungi play a central role in the identification of key forest habitats—smaller areas selected to sustain biodiversity in the managed forest landscape (Timonen et al. 2011). While fungal indicator schemes are generally proposed based on field experience rather

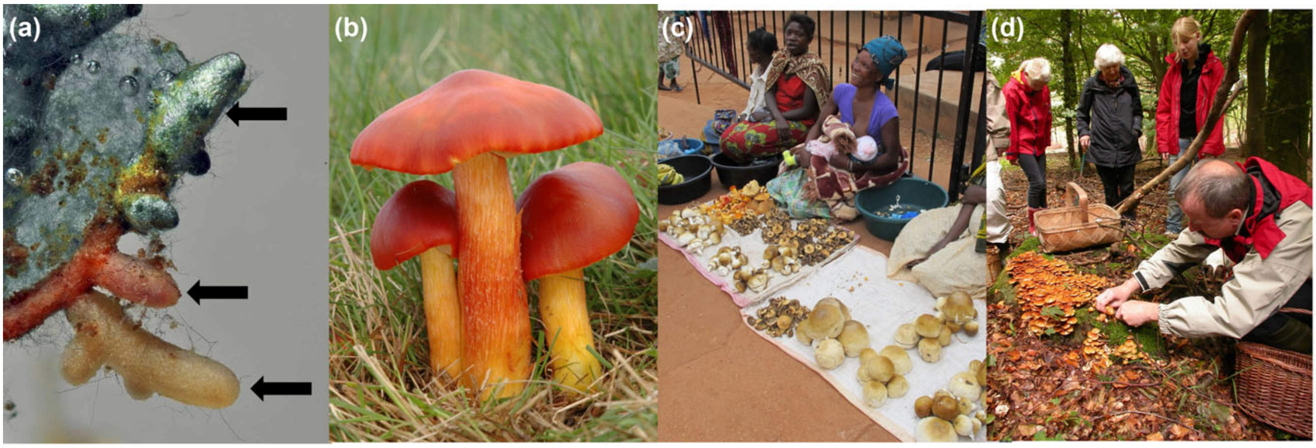

Figure 1. (a) Three different mycorrhizas on European Beech (Fagus sylvatica) *(upper arrow,* Byssocorticium atrovirens*; middle arrow, unknown fungus; lower arrow, Russula sp.) (photo by Jens H. Petersen); (b)* Hygrocybe punicea*, a waxcap species commonly used as an indicator of grassland sites with high conservation value (photo by Nigel Bean); (c) women selling fungi in a street market in Zambia (photo by Maria Härkönen); and (d) a family collecting fungi for food and learning about their identification, near Copenhagen, Denmark (photo by Flemming Rune).*

than hard evidence, several studies confirm the validity of suggested indicator species (e.g., Penttilä et al. 2006; Müller et al. 2007).

Connections between Fungi and Humanity

The links between fungi and people are ancient. Fungi have been used as a source of food, medicine, and tinder for thousands of years. They are features in religious ceremonies, where statues and images of fungi are evident in relicts of ancient civilizations (Rutter 2010). The cultural appreciation of fungi varies across the globe, but in the English speaking world they have been viewed traditionally with suspicion (Arora & Shepard 2008). While this may be one reason fungi have been somewhat overlooked in conservation biology, the situation is clearly changing as people become more aware of the wide variety of uses and actions of fungi.

Wild fungi are a sustainable and renewable resource, which may help turn public opinion in favor of conservation. Today, more than 1100 species of fungi are collected for food or traditional medicine in over 80 countries (Boa 2004). Growing global markets for edible and medicinal mushrooms since the 1980s has led to increased harvesting of many species for subsistence and commercial sale (Fig. 1c). Over-exploitation by harvesters (Minter 2010) and negative effects of harvesting on habitats (Egli et al. 2006) are rare, and positive effects of use, such as increased awareness of fungi and their habitats, yield many benefits for conservation. Their utility provides incentives for conservation because many prized wild fungi are restricted to relatively undisturbed natural areas. Edible wild fungi are increasingly seen as an economic alternative to timber production (Aldea et al. 2012). Even larger economic interests are associated with fungi as principal sources of enzymes, antibiotics, and other chemicals in the biotechnology sector. These interests are expected to increase in the coming century as novel products are discovered from fungi (Erjavec et al. 2012; Rambold et al. 2013). This may help restore links between humanity and nature at a discursive level, even though bioprospecting in general may be overrated as a potential incentive for conservation in practice (Costello & Ward 2006).

In times of increasing concern for disconnectedness between urbanites and the outdoors, collecting wild edible fungi with minimal environmental impacts may be the kind of activity the conservation movement should encourage (Fig. 1d). The tradition of public involvement in the scientific discipline of mycology is long. Even today fungal taxonomists collaborate with amateurs to obtain interesting specimens, and long time-series data from fungal forays have been used in high profile scientific papers of conservation relevance (e.g., Gange et al. 2007). The amount and quality of these data have increased immensely since the development of internet based platforms for recording of species, storage of metadata, including documentation photos, and communication between amateurs and professionals (Halme et al. 2012).

While this development is very similar to what is happening in citizen science based projects on other organisms, high fungal species richness and relatively poorly resolved taxonomy impose new challenges and innovative solutions (Molina et al. 2011). Emery and Barron (2010) involved local non-professional experts in an investigation of the taxonomy and reasons for decline of edible morels in the U.S. Mid-Atlantic. Hence, they provided a link between amateur field knowledge and taxonomic expertise. Some professionals see the increase in amateur mycologists as a threat to professional taxonomy in a time when funding to do basic taxonomic work is shrinking. However, successful citizen science is possible only if skilled professionals can support and train interested amateurs. We fully agree with Korf (2005) and Barron (2011) that mycology as a scientific discipline could benefit from increasing involvement by the public, even though this might imply a reconsideration of research questions and approaches.

Development of New Tools for Biodiversity Monitoring

Rapid developments of high throughput NextGen DNA and RNA sequencing methods are revolutionizing the way fungi can be studied. It is now possible, from a small sample of soil or sawdust, to sample fungal communities, identify known species, and classify unknown species even if the community contains hundreds or thousands of species (Kõljalg et al. 2013). New insights into fungal biodiversity have already emerged, which in some cases have direct conservation relevance (e.g., Kubartová et al. 2012; van der Linde et al. 2012; Ovaskainen et al. 2013). The design of relevant sampling protocols, the processing of massive bioinformatic data sets that include many unknown organisms, and consideration of the relevance of these unknown organisms for conservation are all aspects that require substantial attention. Fungal conservation research strengthened by metagenomics is not happening in isolation, and methodological improvements and subsequent understanding of species distributions, community dynamics, and fungal contributions to processes are likely to have considerable impact in other fields of conservation.

Ways Forward for Fungal Conservation

With an estimated minimum of 1.5 million species worldwide but only 100,000 species named so far, many conservationists might suggest that serious consideration of fungi in conservation is premature. While we agree that the big unknowns in fungal biology are challenging, we also see solutions. Given the magnitude of fungal diversity, the immense variation in life histories and ecological strategies, and the variety of links between fungi and people, multiple case-specific conservation strategies should be considered. For example, in the selection of forest patches for a reserve network, polypores, and lichens might be the most appropriate fungal indicator of conservation value. For education and outreach campaigns, a focus on wild edible and visually striking fungi makes sense. In urban areas, epiphytic lichens are obvious indicators of the state of and changes in air quality. This mirrors the situation in animal conservation, where various taxonomic and functional groups are typically addressed separately, unless interactions or obvious requirements for complementarity call for a complex approach.

Fungal conservation initiatives are currently developing within the mycological community and in national and international conservation organizations in which mycologists participate. We hope the conservation community will welcome these initiatives, collaborate with mycologists, and come to appreciate fungi as a crucial part of nature that needs to be taken into account in efforts to conserve biodiversity on Earth.

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