A Fungal Perspective on Conservation Biology

Essay

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Jacob Heilmann-Clausen[1], Elizabeth S. Barron[2], Lynne Boddy[3], Anders Dahlberg[4], Gareth W. Griffith[5], Jenni Nordén[6], Otso Ovaskainen[7], Claudia Perini[8], Beatrice Senn-Irlet[9], Panu Halme[1,10]

[1]Centre for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Denmark (JHeilmann-Clausen@snm.ku.dk)

[2]Department of Organismic and Evolutionary Biology, 16 Divinity Avenue, Harvard University, Cambridge, MA 02138, USA (barrone@uwosh.edu)

[3]School of Bioscience, Cardiff University, Museum Avenue, Cardiff CF10 3AX, Wales UK (BoddyL@cardiff.ac.uk)

[4]Swedish Species Information Centre, Swedish University of Agricultural Sciences, P.O. Box 7007, S-750 07 Uppsala, Sweden (Anders.Dahlberg@slu.se)

[5] Institute of Biological, Environmental and Rural Sciences, Cledwyn Building, Aberystwyth University, Penglais, Aberystwyth, Ceredigion SY23 3DD, Wales UK (gwg@aber.ac.uk)

[6] Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway; Microbial Evolution Research Group, Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway (jenni.norden@nhm.uio.no)

[7]Department of Biosciences, P.O. Box 65, FI-00014 University of Helsinki, Finland (otso.ovaskainen@helsinki.fi)

[8]BIOCONNET- BIOdiversity and CONservation NETwork, Department of Life Sciences, University of Siena, Italy (claudia.perini@unisi.it)

[9] Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH- 8903 Birmensdorf, Switzerland (beatrice.senn@wsl.ch)

[10]Department of Biological and Environmental Science, University of Jyväskylä, Finland (panu.p.j.halme@jyu.fi)

Corresponding author: Jacob Heilmann-Clausen, Centre for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Denmark (JHeilmann-Clausen@snm.ku.dk), phone +45 23839997

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. But also for other reasons fungal conservation science is growing as an independent field. In this paper we review the role of fungi as actors in ecosystems, and provide an overview of the current state of fungal conservation. On this basis we discuss five areas in which fungi can be readily integrated into, and benefit conservation biology: 1) as providers of habitats and processes important for other organisms, 2) as indicators on desired or undesired trends in ecosystem functioning, 3) in identification of habitats of conservation value, 4) as providers of a powerful links between human societies and the natural world as providers of food, medicine and biotechnological tools, and 5) in the development of novel tools and approaches for conservation in megadiverse organism groups. We hope that the conservation community will value these potentials, and engage in mutualistic connections with mycologists, appreciating fungi as a crucial part of nature

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; Rands et al. 2010; Mace et al. 2012). So far fungi have received limited emphasis in conservation biology (Vesterholt 2008; Minter 2010; Griffith 2012), except as potential threats to ecosystem health, individual species or species groups (e.g. Fisher et al. 2012). Reasons for this neglect are complex but seem mainly to relate to a general suspicious view on fungi in the Anglo-Saxon world, their hidden lifestyle and challenging diversity, and a historical classification as an odd division of the *Plantae.* (Minter 2010). We are certain that the situation is changing, both due to an ongoing revolution in methods to obtain data on fungal species and communities (e.g. Peay et al. 2008; Halme et al. 2012), and because fungi are foundational to a wide variety of ecosystem services.

In this essay we aim to indicate directions towards a full and balanced appreciation of fungi in conservation biology. First, we review the critical roles fungi play in ecosystems. Then we give a brief overview of the current state of fungal conservation. We show that fungal conservation is important in its own right, and further stress how inclusion of the fungal component of biodiversity can benefit conservation in general.

Fungi as ecosystem actors

79 Fungi constitute a megadiverse kingdom, with at least 1.5, but probably as many as 3-5
80 million species, of which only about 100,000 are formally described to date (Blackwell 2011;
81 Hawksworth 2012; Scheffers et al. 2012). Some are unicellular, but the majority form
82 mycelia, which range in size from colonies extending a few millimeters to some of the largest
83 organisms on the planet, e.g. honey fungi (*Armillaria* spp.) whose mycelia can occupy many
84 hectares of forest floor. The majority of fungi are hidden for most of their lives in the
85 substrates which they inhabit. Some form fruit bodies periodically or cause visible symptoms
86 in attacked host-plants, but only lichens are generally visible throughout most of their
87 lifecycle. Dispersal is usually passive, and maintained by microscopic, windborne spores, but
88 aquatic dispersal and animal vectors are important for many species. Profuse spore
89 production may easily lead to the view that fungi generally have much wider distribution
90 ranges and face less dispersal limitation than most other multicellular organisms. Evidence
91 for this idea is diminishing, as new research findings on spore dispersal (e.g. Norros et al.
92 2012) and fungal biogeography based on molecular markers (Taylor 2006; Salgado-Salazar et
93 al. 2013) show that fungi tend to be much less well dispersed and ubiquitous than believed in
94 the past.
95 Despite their hidden lifestyle, fungi maintain crucial processes in all terrestrial
96 ecosystems as decomposers of dead plant tissues and biotrophic partners of almost all
97 terrestrial multicellular organisms. As decomposers fungi are especially prominent in forests
98 and other ecosystems where grazing, fire or human harvesting are not dominant in carbon
99 cycling (Boddy et al. 2008). Plants produce between 5-33 t/ha of organic matter in forest
100 ecosystems every year, with an estimated global carbon pool of 73 petagrams in dead wood
101 (Pan et al. 2011). Most of this organic matter is lignocellulose, an intricate mixture of
102 recalcitrant biopolymers, with fungi being the only organisms possessing the requisite
103 enzymatic capability to mediate its efficient catabolism (Boddy et al. 2008). This process is

104 crucial for the release of nutrients and energy stored in plant litter, so fungi form the basis of
105 soil food chains and are grazed upon directly, or indirectly in plant litter, by a wide range of
106 invertebrate and vertebrate taxa (Stokland et al. 2012). In addition, networks of fungal hyphae
107 are stabilising soil particles into macroaggregates (Caesar-Tonthat 2002) and may thereby
108 protect soils against erosion (Tisdall et al. 2012).

109 Fungi are involved in diverse mutualistic associations. Lichenized fungi associated
110 with green algae or cyanobacteria, are highly stress-tolerant and mediate most primary
111 production and nitrogen fixation in desert and polar ecosystems, that covers 6 % of the
112 Worlds surface (e.g. Belnap 2002; Haas & Purvin 2006). They also dominate other
113 microhabitats in other climate zones such as tree trunks, rock surfaces and living leaves of
114 rainforest trees (Scheidegger & Werth 2009). Most plants (ca. 90% of species) are reliant on
115 mycelial networks intimately connected with their roots -mycorrhizas- for the uptake of
116 water, N, P and mineral nutrients from soil (Smith & Read 2008). In return for the water and
117 nutrients, mycorrhizal fungi receive substantial amounts of sugars from their plant partners,
118 typically 15 to 30 % of the net primary production (Chapin et al. 2011).

119 Mycorhizal fungi are not only important for nutrient cycling, but also for mineral
120 weathering and carbon storage in forest ecosystems (Courty et al. 2010; Clemmensen et al.
121 2013). Further, they are tightly involved in plant competition, and because different groups of
122 fungi have very different enzymatic capacities, changes in plant composition mediated by
123 natural or anthropogenic processes might result in dramatic shifts in ecosystem processes
124 (Averill et al. 2014).

125 More cryptically, the internal tissues of all vascular plants host diverse communities
126 of asymptomatic fungal endophytes, of which some are mutualistic and prevent attacks from
127 pathogens and herbivores, while other are decomposers with a latent invasion strategy (e.g.
128 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, fungal endophytes are not clearly delimited from fungi classified as pathogens. In quite many cases beneficial effects to the host may shift to pathogenic, due to environmental changes or imbalance in co-evolutionary processes. For example, the recent outbreaks of ash-dieback in Europe are caused by the endophytic *Hymenoscyphus pseudoalbidus,* which most likely originates in Eastern Asia where it lives in non-pathogenic association with Manchurian Ash (*Fraxinus mandschurica*) (Zhao et al. 2012). In parts of Europe it has now replaced the native *Hymenoscyphus albidus*, that used to be a harmless latent decomposer of dead leaves and petioles of the European Ash (*F. excelsior*)(Pautasso et al. 2013). Other biotrophic fungi associate with animals, as mutualists, e.g. in the rumen of herbivorous mammals or as a feeding source for insect larvae in wood, or as parasites.

Sadly the public perception, and perhaps that of many conservation biologists, is that fungi are extremely harmful because of the pathogenic ability of a few species (Fisher et al. 2012). Well known examples include the apparent extinction of several 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 even suggest that 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). Interestingly, many outbreaks of pathogenic fungi are caused or strongly reinforced by human manipulations, not least the unintentional movement of fungal species around the globe (e.g. Brasier 2008).

Current state of fungal conservation

The factors that threaten susceptible fungal populations are essentially the same as those threatening animals and plants, including the degradation, loss and fragmentation of natural and managed habitats, climate change, 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. We identify several reasons for this. First of all, the boreal zone consists largely of coniferous forests, which provide a wealth of niches for fungal species, but host relatively few vascular plants and larger animals. Secondly, and perhaps linked to the scarcity of large charismatic animals, the tradition to focus more on habitats than on specific species is deeply rooted in Fennoscandia (Raunio et al. 2008). In practice, species from many species groups are used together to identify and prioritize conservation measures. As discussed in the next section, cryptogams are well suited as indicator species to identify sites, in particular forests, with specific conditions and histories. Thirdly, Fennoscandia has a long tradition in fungal taxonomy and a good community of amateur field biologists, which has resulted in a large and increasing knowledge on the ecology and distribution of macrofungi that has formed the basis for the successful red-list evaluation of more than 5000 species (Rassi et al. 2010).

Fungal red-listing is now widely used for management and conservation activities across Europe; according to Dahlberg & Mueller (2011) only two of 35 national red lists for fungi were produced in other parts of the world (New Zealand and Japan). A few countries including Finland, Norway, Sweden and the UK have launched action plans to protect specific fungal habitats and species, and in at least 12 European countries there are examples of considering fungi in selection and prioritization of nature reserves (Senn-Irlet et al. 2007; Dahlberg et al. 2010). Outside of Europe and the Pacific Northwest region of the USA

(Molina 2008) initiatives and strategies to conserve fungal biodiversity are more scattered (but see Minter 2001; Buchanan & May 2003; Manoharachary et al. 2005; Abdel-Azeem 2010), and only three fungal species are currently globally red-listed. However, the situation is changing, and the five fungal specialist groups of IUCN aim to have several hundred fungal species globally red-listed 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 International Union for Conservation of Nature (IUCN). Since 2007, fungal conservation committees or groups have also been established in Africa, South America and the US (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.

What can fungi offer conservation biology?

Current approaches to conservation acknowledge that human wellbeing 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 (Pringle et al. 2011), but the fundamental role fungi have as regulators of ecosystem processes in terrestrial ecosystems places them centrally in the development of sustainable land use (Parker 2010; Mace et al. 2012). However, it is just as evident that the majority of threatened fungi do not contribute, and cannot even survive, in areas managed for timber and crop production. Hence the arguments for their conservation should be based on arguments that are related to other ecosystem services, some of which might be impossible to quantify in economic terms. We

204 believe that fungi deserve conservation in their own right, but below we will review how
205 conservation can benefit in general by the inclusion of fungi (Fig. 1).
206
207 Fungi as providers of services for other organisms
208 As described in the previous section, fungi are the drivers of several key processes in natural
209 ecosystems. Most of these are maintained by larger guilds of fungi, like the recycling of
210 nutrients from dead wood, or plant nutrition maintained by mycorrhizal fungi. Within guilds,
211 fungal communities are often very species rich, suggesting high levels of functional
212 redundancy. Both experimental (e.g. Strickland et al. 2009; Fukami et al. 2010) and
213 explorative studies (e.g. Taylor et al 2014) have reported high levels of niche differentiation
214 and less redundancy than expected in fungal communities, indicating that species identities
215 matter in major ecosystem processes where fungi contribute.
216 In other cases specific or smaller set of fungal species play key roles for other biota.
217 Fungi provide a principal food resource for many organisms, including mammals, orchids
218 and insects. In many cases associations are species specific or strongly selective, implying
219 that understanding of the fungal part of the association is crucial for the conservation of the
220 dependent feeders (e.g. Claridge & May 1994; Pyare & Longland 2002; Komonen 2003;
221 Bailarote et al. 2012). Polypores and other long-lived fleshy fruitbodies are particular rich
222 habitats for dependent insects, especially beetles and diptera. For example, the Dryad's
223 Saddle (*Polyporus squamosus* (Huds.) Fr.), hosts over 246 beetle species in Europe (Benich
224 1952). Other fungi are involved in the formation of microhabitats, such as cavities in trees
225 that are critical for hollow breeding birds, mammals, arthropods and epiphytes (e.g. Parsons
226 et al. 2003; Fritz & Heilmann-Clausen 2010; Remm & Lõhmus 2011; Cockle et al. 2012). In
227 some cases these associations may be species specific (e.g. Jackson & Jackson 2004).

228

229 Fungi as indicators of ecosystem processes

230 With their narrow and thin-walled hyphae fungi are exposed to chemicals in the environment
231 and highly sensitive to microclimatic gradients, a fact that has been utilized in developing
232 indicator schemes based on fungi. Lichens are among the most sensitive organisms regarding
233 changes in air quality. In fact, the earliest record of biodiversity loss resulting from human
234 industrial activity was made by Thomas Pennant in 1773 who observed the decline of lichens
235 as a result of copper smelting at Parys Mountain, Wales (Pennant 1781). The differential
236 sensitivities of lichens to SO_2 and other airborne pollutants have since been widely used as a
237 proxy measure of air quality in both urban and natural habitats (Conti & Cecchetti 2001;
238 Nimis et al. 2002).

239 Non-lichenized fungi are also affected by SO_2 pollution, but anthropogenic nitrogen
240 pollution is now the most pervasive threat, with the decline of some ectomycorrhizal species,
241 e.g. stipitate hydnoids and also *Cortinarius* spp. being particularly dramatic, though more
242 widespread changes in species composition in polluted areas are of equal concern (Arnolds
243 2001; Lilleskov et al. 2011).

244 The effects of global climate change on fungi are difficult to quantify, but it is
245 apparent that the warming climate over recent decades has altered the phenology of fungal
246 fruiting (Kauserud et al. 2012). For example, many fungi previously known to fruit only in
247 the fall now also fruit in spring, and mycorrhizal fungi associated with deciduous trees now
248 fruit later in the year. Changes in fungal community structure provide an early warning of
249 changing ecosystem processes, but so far there have been few efforts to implement this in
250 standardized monitoring schemes. Broadly, fungi constitute the most visible link to the vast
251 biodiversity underground, and are basal to the highly diverse decomposer food chains.

252 Incorporating fungi into ecosystem level indices such as the biodiversity intactness index
253 (Scholes & Biggs 2005) and the living planet index (Loh et al. 2005), which so far neglected
254 decomposers in general, would greatly enhance the value of these indices. Rapid advances in
255 the use of DNA-based methods for monitoring fungal communities (Schoch et al. 2012;
256 Lindahl et al. 2013) and increasing understanding of their functions, will likely facilitate the
257 use of fungi as bio-indicators of soil status and processes.
258

259 Fungi as indicators in conservation planning

260 The very specific habitat requirements of fungi make them well-suited as indicators for
261 selecting conservation areas and monitoring their status. A fungal angle on habitats simply
262 expands our understanding of the biotic space, and puts emphasis on microhabitats and
263 processes that are pivotal for biodiversity, but easily overlooked if fungi are not addressed.
264 For instance, specialized wood-inhabiting fungi may be absent from otherwise valuable
265 woodland habitats due to the lack of veteran trees and dead wood, and may become extinct at
266 the landscape scale if remaining old growth habitats are fragmented (Nordén et al. 2013).
267 Similarly, some ectomycorrhizal and lichenized fungi are highly sensitive to breaks in forest
268 continuity, and may be lost from forest ecosystems if mature trees are not retained through
269 rotations (Coppins & Coppins 2002; Rosenvald & Lõhmus 2008). These processes are also
270 important for many other organisms, including arthropods, molluscs and microfauna, but in
271 practice fungi will often be the easiest group to monitor.

272 Especially in Europe, several indicator schemes based on fungi have been suggested
273 to assess the conservation value of forests and grasslands (e.g. Coppins & Coppins 2002;
274 Heilmann-Clausen & Vesterholt 2008); and in Sweden and the Baltic countries fungi have
275 played a central role in the identification of key forest habitats – smaller areas selected to

lifeboat biodiversity in the managed forest landscape (Timonen et al. 2011). While fungal indicator schemes are generally proposed based on field experience rather than hard evidence, several studies have posthoc confirmed the validity of several indicator species (e.g. Penttilä et al 2006; Müller et al. 2007).

Connections between fungi and humanity

The cultural value and public appreciation of fungi varies in different parts of the world, but in the English-speaking world they have traditionally been viewed with great suspicion. While this might be one reason that fungi have been somewhat overlooked in conservation biology, the situation is clearly changing as people become more aware of the wide variety of uses of fungi. In reality links between fungi and people are ancient. Fungi have been used as food-sources, medicine, crafts, arts and tinder for thousands of years. They also feature in religious ceremonies, where fungal statues and images are evident in relicts of ancient civilizations and Stone Age art (Rutter 2010).

Wild fungi are a sustainable and renewable resource, which may help to turn public opinion in favor of habitat conservation. Today, more than 1100 wild fungi are collected for food or traditional medicine in over 80 countries worldwide (Boa 2004). Increasing global markets for edible and medicinal mushrooms since the 1980s has led to increased harvesting of many species both for subsistence use and for commercial sale. Over-exploitation by harvesters (Minter 2010), or negative effects of harvesting on habitats (Egli et al. 2006) are rare, and positive effects of increased use, such as increased awareness of fungi and their habitats, yield many benefits for conservation. Their utility provides incentives for conservation, as many prized wild fungi are restricted to relatively undisturbed natural habitats. Indeed, edible wild fungi are increasingly seen as an economic alternative or

300 supplement to timber production in Europe and the United States (e.g. Aldea et al. 2012).
301 Even larger economic interests are associated with fungi as principal sources of enzymes,
302 antibiotics and other chemicals in the biotechnology sector. These interests are expected to
303 increase considerably in the coming century as novel products are discovered from fungi
304 (Erjavec et al. 2012; Rambold et al. 2013). This might help restore links between humanity
305 and nature at a discursive level, even though bioprospecting in general may be overrated as a
306 potential incentive for conservation in practice (Costello & Ward 2006).

307 In times of increasing concern for disconnectedness between growing urban
308 populations and the outdoors, the simple joy of collecting wild edible fungi with minimal or
309 no negative environmental impacts may be exactly the kind of activities that the conservation
310 movement should be encouraging through education and a focus on sustainability. The
311 tradition of public involvement in the scientific discipline of mycology is long. Even today
312 many fungal taxonomists collaborate with amateurs to obtain interesting specimens, and more
313 recently long time-series data from fungal forays have been used in high profile scientific
314 papers of conservation relevance (Gange et al. 2007; Kauserud et al. 2012). The amount and
315 quality of fungal data collected is increasing immensely through the development of internet
316 based platforms for species recording allowing easy storage of metadata, including
317 documentation photos, and facilitating communication between amateurs and professionals
318 (Halme et al. 2012).

319 While this development is very similar to what is happening in citizen science based
320 projects on birds, plants and butterflies, high fungal species richness and relatively poorly
321 resolved taxonomy impose new challenges and innovative solutions (Molina et al. 2011). For
322 instance, Emery and Barron (2010) involved local non-professional experts to investigate the
323 taxonomy and possible reasons for decline of edible morels in the US Mid-Atlantic Region,

hence shortcutting the link between amateur field knowledge and taxonomic expertise. Some professional mycologists may see the growth of fungal amateur activity as a threat in a time where funding to do basic taxonomic work is shrinking. However, successful citizen science is only possible if backed by skilled professionals that can support and train the interested amateurs. We fully agree with Korf (2005) and Barron (2011) that the limited environment of professional mycologists could benefit by increasing involvement with the public, even though this might imply a reconsideration of research questions and approaches.

Development of new tools for biodiversity monitoring

Finally, we believe that the current knowledge gap in fungal biodiversity may prove to be an important driver in the development of novel tools with a broad relevance in conservation biology, especially molecular analyses making use of DNA barcodes for species identification. In part due to the rapid developments of high throughput 'NextGen' DNA sequencing, remarkable 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). A larger challenge is to put such information into an appropriate conservation context and to combine it with other types of ecological knowledge. Designing relevant sampling protocols for fungi, processing massive bioinformatic data sets that include many unknown organisms (Hibbett et al. 2011), and considering relevance for other organismic groups are all aspects of this emerging suite of methods that require significant consideration moving forward.. Hence fungal conservation research strengthened by metagenomics is not happening in isolation, and methodological improvements and subsequent understanding of species distributions, dynamics and contributions to processes are likely to have considerable impact in other fields of conservation biology.

Conclusions

Fungal conservation science is maturing as its own field, and has much to offer as conservation biology moves from addressing single species to an integrative ecosystem based approach. Fungi provide the most visible link to the vast biodiversity underground, and are basal to the highly diverse decomposer food chains. In addition they are key mutualist partners of plants and animals, playing fundamental regulating roles in all terrestrial ecosystems. Incorporating mycological knowledge is crucial in the development of sustainable practices in agriculture and forestry, in assessments of the state of natural ecosystems, and in conservation planning that intends to cover all major aspects of biodiversity.

Socially, due to their attractive fruit bodies, fungi represent a rich source of wonderment, and are additionally valuable as food, in traditional medicine and as a source of bioactive compounds. In most cases, modest collecting of wild fungi is non-detrimental to ecosystems, and an increasing understanding of fungi may indeed help conservation to gain broader understanding in rural as well as urban settings.

With an estimated 1.5 million species worldwide but only 100.000 species named so far, many conservationists might suggest that seriously consideration fungi in conservation is premature. While we agree that the big unknowns in fungal biology are challenging, we also see obvious 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, a single approach to fungal conservation is untenable and undesirable. Rather, a variety of case specific strategies should be considered. For example, in the selection of forest patches for a reserve network, polypores might be the most appropriate fungal tool. When considering

372 education and outreach campaigns, a focus on wild edibles and visually striking fungi makes
373 sense. When assessing effects of air pollution in urban setting, epiphytic lichens are the
374 obvious choice. This mirrors the situation in animal conservation, where various taxonomic
375 and functional groups are typically addressed separately, unless interactions or obvious
376 requirements for complementarity call for a complex approach.

377 Fungal conservation initiatives are currently under development within the
378 mycological community, and in different national and international organizations and
379 institutions where mycologists participate. We hope that the conservation community will
380 welcome these initiatives, and engage in mutualistic connections with mycologists,
381 appreciating fungi as a crucial part of nature that needs to be taken into account in our efforts
382 to conserve biodiversity on Earth.

383

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560 Figure 1. Four examples emphasizing how fungi provide added value in biodiversity
561 conservation: (1) They provide and give direct insight into important supporting ecosystem
562 services including nutrient cycling, and mycorrhizal symbiosis that enhance plant nutrition
563 and resistance to drought, soil pollution and pathogens (A, Three different ectomycorrhizas
564 on European Beech (*Fagus sylvatica* L.)). (2) They are useful as indicators when evaluating
565 the conservation potential of conservation areas or the conservation outcome of conducted
566 management actions (B, *Hygrocybe punicea* (Fr.) P. Kumm., a waxcap species that is
567 commonly used as an indicator of grassland sites with high conservation value). (3) They
568 play an important role in developed countries in providing recreational values and
569 reconnecting urban citizens with nature (C, A family collecting fungi for food and learning
570 about their identification, near Copenhagen, Denmark). (4) They provide a sustainable
571 income from intact forests for the local people in developing countries and can thus play a
572 role in turning local attitudes positive towards conservation areas (D, women selling fruit
573 bodies of native mycorrhizal fungi in a street market in Zambia). Photo courtesy of Jens H.
574 Petersen (A), Nigel Bean (B), Flemming Rune (C), Marja Härkönen (D).