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The history and future of fungi as biodiversity surrogates in forests

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ABSTRACT

Biodiversity surrogates are commonly used in conservation biology. Here we review how fungi have been used as such in forest conservation, emphasizing proposed surrogate roles and practical applications. We show that many fungal surrogates have been suggested based on field experience and loose concepts, rather than on rigorously collected scientific data. Yet, they have played an important role, not only in forest conservation, but also in inspiring research in fungal ecology and forest history. We argue that, even in times of ecosystem oriented conservation planning and molecular tools to analyze fungal communities, fruit bodies of macrofungi have potential as convenient conservation shortcuts and easy tools to communicate complex biodiversity for a broader audience. To improve the reliability of future fungal surrogates we propose a three step protocol for developing evidence based schemes for practical application in forest conservation.

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1. Introduction

Nature managers need reliable information on biodiversity to be able to make efficient conservation decisions. However, conducting a full biodiversity survey is practically impossible even for very small areas (Basset et al., 2012), and usually conservation planning needs to be based on information on large, even nationwide or cross-border areas (Lindenmayer and Likens, 2011). Therefore, in the lack of high resolution high coverage data on biodiversity, conservation decisions are usually based on some proxies of the conservation value of relevant areas. In an optimal planning situation, these proxies, preferably containing data on several different species groups (Westgate et al., 2014), are downloaded in spatial conservation planning software and the decision is based on a systematic analysis involving factors like habitat quality, connectivity, complementarity and cost efficiency (Teeffelen et al., 2006; Moilanen et al., 2011). However, often the information needed for

such an analysis is fragmentary or lacking, or time constraints are too strict for such a holistic approach. One type of proxy is surrogate species, which according to Caro (2010), “are used to represent other species or aspects of the environment to attain a conservation objective”.

In reality, surrogate species are used in various ways and for various purposes, and the terminology has historically been highly confusing. Based on Caro (2010), who has made a serious effort to disentangle the most common surrogate types and their usages, the following types can be distinguished:

Biodiversity indicators are proposed to indicate the richness of a larger species group, other species group(s) or even the whole other biota (Fig. 1; Rodrigues and Brooks, 2007; Sálek et al., 2015). Biodiversity indicators have been used to recognize and delineate biodiversity hotspots on the continental to global scale (Orme et al., 2005), and to assist reserve site selection on the national to regional scale (Caro, 2010).

Umbrella species are proposed to serve as conservation umbrellas for a number of other species with shared habitat or management requirements (Roberge and Angelstam, 2004; Branton and Richardson, 2011). Related hereto, the *Focal species* concept is basically a multispecies umbrella species approach, where a set of

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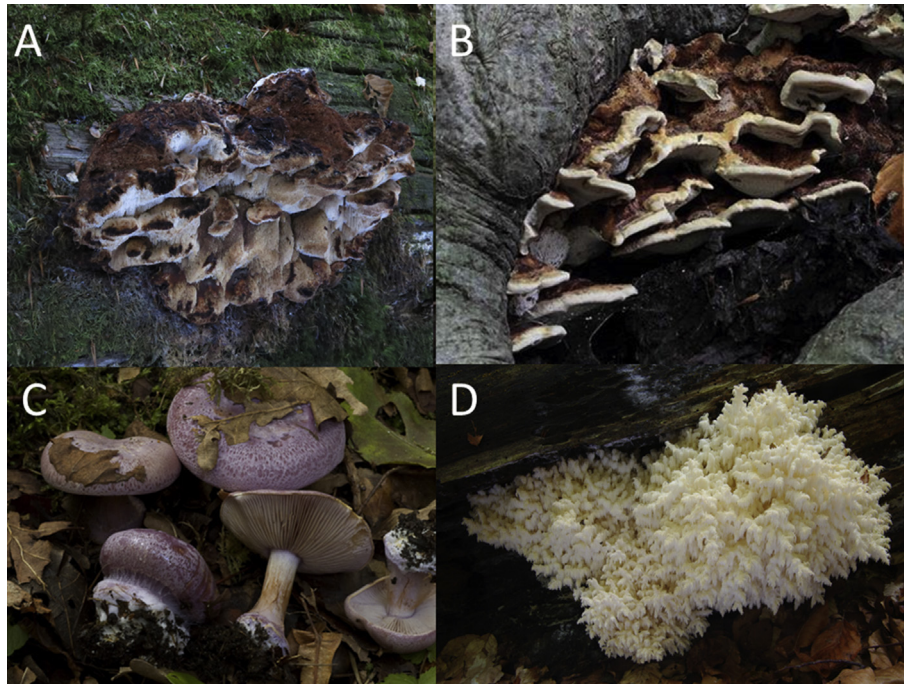


Fig. 1. Examples of suggested fungal surrogates: (A) *Amylocystis lapponica* is a widely used indicator of old-growth forest habitats, and may serve as a suitable umbrella species for conserving threatened biota associated with old-growth spruce forests (see Nordén et al., 2013). (Czech Republic, Boubínský prales virgin forest, photo Jan Holec); (B) *Inonotus cuticularis* is a key agent in forming hollows in living beech trees, and can hence be considered a potential fungal keystone species, responsible for the creation of important habitats for threatened beetles (Müller et al., 2014). (Denmark, Hesede Skov, photo Thomas Kehlet); (C) Based on nested subset patterns *Cortinarius sodagnitus* was identified by Jeppesen and Frøslev (2011) as a good biodiversity indicator for communities of *Cortinarius* subg. *Phlegmacium* species forming ectomycorrhizas with deciduous trees on clayey or calcareous soils (Sweden, Bohuslän, photo Thomas Stjernegaard Jeppesen); (D) *Hericium coralloides* has been promoted as an indicator species several times and has obvious flagship species qualities, due to its attractiveness and large size. However, in this issue Abrego et al., (2016, 2017) show that actually it is not strictly dependent on well-connected old-growth forests (Czech Republic, Boubínský prales virgin forest, photo Jan Holec).

selected species are proposed to have specific life history characteristics that are expected to confer protection to other species that are facing similar threats if addressed properly in conservation planning (Nicholson et al., 2013).

Keystone and engineering species are defined as species with especially important roles in the ecosystem. Their presence is often needed for maintaining important aspects of ecosystem functioning and, as surrogates, their presence in an ecosystem simply indicates that these roles are played (Paine, 1995; Caro and O'Doherty, 1999).

Flagship and iconic species are primarily conservation awareness raising tools and used mostly to target public interest towards endangered habitats or species (Andelman and Fagan, 2000; Caro, 2010).

Ecological disturbance indicators are proposed to indicate a general effect of a certain disturbance in the environment whereas *cross-taxon disturbance indicators* are proposed to indicate the effect of a disturbance specifically on some certain taxa other than the indicator group itself (Caro, 2010). Usually these indicators are used to monitor the effects of negative disturbances such as extensive pollution. Closely related to disturbance indicators, different concepts of ecological indicators have been proposed. For example, Ellenberg indicator values (Ellenberg et al., 1991) are well-known tools to identify ecological conditions especially in plant communities. Ellenberg values have been developed to estimate the position of known communities along gradients of humidity, soil productivity, pH, continentality and other important factors, without taking direct measurements (see for example Dupouey et al., 2002; Seidling and Fischer, 2008; Simmel et al., 2017). These approaches should be separated from biodiversity surrogate approaches because of their different focus and purpose, even if

they are highly relevant in monitoring habitat quality, and not least changes in habitat quality over time.

In this paper we focus on non-lichenized fungi as biodiversity surrogates in forest habitats. We first review how fungi have been used as biodiversity surrogates historically. We continue with a critique on proposed surrogate schemes conceptually, and in relation to the current knowledge of good surrogate schemes, and our own experience. Finally, we suggest a proposal for better protocols with a special focus on fungi as surrogate agents. Our proposal is divided in 3 separate steps that should, in our opinion, be followed to reach a justified and reliable surrogate system.

2. The history of fungi as practical surrogates in forest conservation

The use of fungi as biodiversity surrogates in forest conservation was initiated in North Europe in the 1990s (Høiland and Bendiksen, 1991; Vesterholt, 1991; Karström, 1992; Kotiranta and Niemelä, 1996; Parmasto and Parmasto, 1997, Table 1). The proposal of fungal surrogate species was stimulated by increasing awareness of modern forestry as a threat to forest biodiversity, and was fueled by the fact that boreal forests have a low diversity of vascular plants (see Heilmann-Clausen et al., 2015). In contrast, fungi are often more visible, very diverse and play important roles in boreal forest ecosystems as decomposers and mycorrhizal symbionts, and many are associated with old-growth forest characteristics, like the presence of large dead wood and undisturbed forest soils. Typically, the selection of species was based on the long-time experience of leading field mycologists combined with studies of fungal diversity in selected areas or monitoring plots. The surrogate lists were made for evaluation and comparison of various forest stands with the aim

Table 1

Fungal biodiversity surrogates proposed for assessing conservation value of forest habitats in Europe. *Scale* refers to the area from which the authors obtained data, or proposed the scheme to be used. *No. of indicators* refers to the number of listed surrogate species. *Stated focus* shows what authors have stated the species to indicate. *Surrogate concept* shows our classification of the scheme following [Caro's \(2010\)](#) guidelines for biodiversity surrogates. Scientific evidence indicates if there has been some statistical analysis testing the validity of the scheme.

Title	Reference	Forest type(s)	Scale	No. of Indicators	Groups included	Stated focus	Surrogate concept	Scientific evidence
Wood-inhabiting fungi as indicators of nature value in European beech forests	Christensen et al. (2004)	Beech forests	Europe	21	Wood-inhabiting fungi	biotic integrity, conservation value	focal species	Abrego et al. (2015)
Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe	Odor et al. (2006)	Beech forests	Europe	100	Wood-inhabiting fungi	conservation value (proxy for red-list status)	biodiversity indicator	
Naturnähezeiger – Holzbewohnende Pilze als Indikatoren für Strukturqualität im Wald	Blaschke et al. (2009)	All types of Central European forests	Central Europe	68	Wood-inhabiting fungi	structural quality, nature value	focal species	
Threatened polypores in Finland. Second revised edition	Kotiranta and Niemelä (1996)	Coniferous boreal forests	Finland	33	Wood-inhabiting fungi	biotic integrity, conservation value	focal species	Nordén et al., 2013
Hot spots, indicator taxa, complementarity and optimal networks of taiga	Virolainen et al. (2000)	Boreal coniferous forests	Finland	29	Polypores	cross taxon species richness (hot-spot and complementarity)	biodiversity indicator	An optimizing algorithm to show the relationships
Quantifying the indicator power of an indicator species	Halme et al. (2009a)	White-backed woodpecker territories	Finland	5	Polypores	presence of specific red-listed polypores	biodiversity indicator	Selection based on an analysis in the same paper
Perennial polypores as indicators of annual and red-listed polypores	Halme et al. (2009b)	Boreal forests	Finland	not specified	Polypores	species richness of polypores	biodiversity indicator	Analysis of covariance to show the relationship
Indicator fungi	Bonsdorff et al. (2014)	15 different boreal forest types	Finland	545	Macrofungi, especially mycorrhizal	Evaluating habitat's conservation value	focal species	
Wood-inhabiting fungi as indicators of continuity in spruce forests in eastern Norway	Bredesen et al. (1997)	Spruce forests	Eastern Norway	6	Wood-inhabiting fungi	Continuity in the presence of dead wood	focal species	Testing of indicator value in paper
Exploring potential biodiversity indicators in boreal forests	Jonsson and Jonsell (1999)	Boreal spruce forest	Sweden	42	Polypores	cross taxon species richness	biodiversity indicator	Test for nested subset patterns
Indicator species for assessing the nature conservation value of woodland sites– A flora of selected cryptogams	Nitare (2000)	Different boreal forest types	Sweden	139 taxa	Macrofungi	nature/ conservation value	focal species	
Knoldslørhatte (Cortinarius underslågt Phlegmacium) som indikatorer for en type værdifulde løvskogslokaliteter	Vesterholt (1991)	Nemoral deciduous forests	Denmark	32	<i>Cortinarius</i> subg. <i>Phlegmacium</i>	conservation value	focal species	
Fungi on beech logs - indicators of valuable deciduous forest habitats	Heilmann-Clausen and Christensen (2000)	Beech forests	Denmark	42	Wood-inhabiting fungi	conservation value	focal species	
Knoldslørhatte som indikatorarter gennem 20 år	Jeppesen and Frøslev (2011)	Nemoral deciduous forests	Denmark	6	<i>Cortinarius</i> subg. <i>Phlegmacium</i>	species richness of <i>Cortinarius</i> subg. <i>Phlegmacium</i>	biodiversity indicator	A simple nested subset analysis, supporting the indicator value
25 danske indikator-arter (svampe, mosser og laver) til overvågning af skovhabitat-typer (NOVANA).	Rune et al. (2007)	Natura 2000 forest habitat types in Denmark	Denmark	13	Wood-inhabiting fungi	conservation status	focal species	Ejrnæs et al., 2009
Lignicolous Aphyllophorales of old and primeval forests in Estonia 1	Parmasto and Parmasto (1997)	Southern Taiga Zone forests (pine, spruce)	Estonia	42	Macrofungi, mostly wood-inhabiting	primeval forest conditions (continuity and lack of disturbance)	focal species	
Fungi as indicators of primeval and old-growth forests deserving protection	Parmasto (2001)	Boreal and nemoral old-growth forests	Estonia	49	Macrofungi, mostly wood-inhabiting	biotic integrity, conservation value	focal species	
Habitat indicators for cavity-nesters: The polypore <i>Phellinus pini</i> in pine forests	Löhmus (2016)	Pine-dominated forests	Estonia	1	<i>Phellinus pini</i>	diversity of cavity-nesting birds	keystone/ engineering species	Multivariate models in the paper
Developing tools for assessing fungal interest in habitats. 1: beech woodland saprotrophs	Ainsworth (2004)	Beech forest	UK	30	Wood-inhabiting fungi	conservation value	focal species	

(continued on next page)

Table 1 (continued)

Title	Reference	Forest type(s)	Scale	No. of Indicators	Groups included	Stated focus	Surrogate concept	Scientific evidence
Relict fungi of primeval forests in the Świętokrzyskie Mountains (Central Poland)	Łuszczynski (2003)	Pine, oak, beech, beech-fir forests	Poland: Świętokrzyskie Mountains	30	Macrofungi	primeval forest conditions	focal species	
Characteristic species of important sites for beech-inhabiting fungi in Belgium and The Netherlands	Walley and Veerkamp (2005)	Beech forest	Benelux	21	Wood-inhabiting fungi			
Mykologischer Vergleich zwischen Naturschutzgebieten und Forstflächen	Nuss (1999)	Montane beech-fir-spruce forest	Germany: Bavaria	57	Macrofungi, mostly wood-inhabiting	conservation value	focal species	
Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany	Müller et al. (2007)	Beech forest	Germany: southern part	18	Wood-inhabiting fungi	management intensity	focal species	Test based on indicator species analysis
Auf natürliche, vom Menschen nur minimal beeinflusste Vegetation beschränkte Großpilze	Holec (2003)	Central European montane ecosystems	Czech Rep.: Bohemian Forest	26	Macrofungi, mostly wood-inhabiting	primeval forest conditions	focal species	
Interesting macrofungi from the Eastern Carpathians, Ukraine and their value as bioindicators of primeval and near-natural forests	Holec (2008)	Montane beech-fir-spruce and ravine forests	Ukraine: Eastern Carpathians	10	Macrofungi, mostly wood-inhabiting	primeval forest conditions	focal species	
An attempt to a list of indicator fungi (Aphyllophorales) for old forests of beech and fir in former Yugoslavia	Tortić (1998)	Old and primeval beech-fir-spruce forests	former Yugoslavia	42	Wood-inhabiting fungi	primeval forest conditions	focal species	

to identify and protect the ones with the highest conservation value. Forests with long, uninterrupted presence (i.e. continuity, also called “old-growth”, “pristine”, “virgin” etc.) (Nordén et al., 2014) were the focal habitats and the lists mostly contained rare and often threatened wood-inhabiting fungi, most commonly polypores. Closely related, in some initiatives fungi were proposed to indicate biodiversity refugia, i.e. the last safe harbors for old-growth associated species in heavily managed landscapes (Łuszczynski, 2003; Holec et al., 2015a).

The first lists of fungal surrogates were compiled for selected regions (e.g. Bredesen et al., 1997: eastern Norway) or countries (e.g. Parmasto, 2001: Estonia). The first attempt to cover a whole continent was made by Christensen et al. (2004: European beech forests). Their list is widely used for comparison of beech forests across Europe, but sometimes with regional modifications (e.g. Ainsworth, 2004: UK; Walley and Veerkamp, 2005: Belgium and The Netherlands; Adamčík et al., 2016: Slovakia). The first list covering all forest types in a country was produced by Blaschke et al. (2009: Germany). Its aim was to indicate the forest stand naturalness. A recent list from Finland (Bonsdorff et al., 2014) focuses on the conservation value of forest sites by inclusion of fungi characteristic of valuable biotopes across the full gradient of boreal forest types. Most of the proposed surrogate lists have focused mainly on wood-inhabiting species, but Nitare (2000) and Bonsdorff et al. (2014), for example, included fungi with different trophic strategies. Only a few schemes have focused strictly on mycorrhizal fungi (e.g. Vesterholt, 1991; Jeppesen and Frøslev, 2011).

In many cases, Red Listed species have been directly used to document conservation value (e.g. Heilmann-Clausen and Christensen, 2000), but an obvious weakness with fungal Red Lists provided so far is their national scope, making comparisons across larger regions biased (Dahlberg and Mueller, 2011). To overcome this, Odor et al. (2006) proposed a list of “fungi of special interest” on the scale of continental Europe to be able to discuss how beech forests were affected by forest management and forest

fragmentation in different countries from Denmark to Slovenia, and to identify regions of the highest conservation value. Data on previously published fungal surrogate schemes in forest ecosystems are given in Table 1.

In Fennoscandia, some of the proposed surrogate species lists are widely used in active forest conservation work, even though they lack legal status in any of the countries. In Finland, the “old-growth forest indicator polypores”, proposed by Kotiranta and Niemelä (1996) have been perhaps the most commonly surveyed species group in conservation oriented forest biodiversity programs (see for example Kunttu and Halme, 2008), and collected information based on the list is commonly used in conservation decisions. Similarly, in Sweden and Norway different indicator lists have been widely used to evaluate the conservation value of forest habitats based on a Swedish list focusing on several different forest habitat types (Nitare, 2000) together with the afore mentioned Finnish list.

Outside Fennoscandia surrogate schemes have been used only to a limited extent. In Estonia the conservation biologists working for the government use a list of fungal surrogates to identify woodland key habitats, which is a North European conservation concept focusing on the protection of especially important forest sites (Timonen et al., 2010). This list includes several fungal species and has a legal status (Anonymous, 2010). In Russia, the extensive manuals by Andersson et al. (2009a, 2009b) are used in conservation value evaluation (Sorokina et al., 2013) to avoid cutting in the most valuable sites, although their legal status is indirectly based on the general praxis. In 2015, 2016, official methodology for assessing conservational value of habitats at Sites of Community Importance using surrogate species of fungi (in addition to vascular plants and selected groups of animals) is in preparation in the Czech Republic and will soon be used in site selection praxis (J. Holec, pers. comm.). In this case fungi are considered a very useful group indicating habitat variables which are not so obviously indicated by other organismal groups (e.g. forest continuity).

3. Critique and testing of proposed surrogate schemes

As indicated above most fungal surrogate lists have been proposed to raise awareness of threatened forest habitats suggesting some species to be more ‘special’ or ecologically demanding than others. In many cases it has not been made explicit if the selected species were surrogates of biodiversity or rather umbrella or focal species well suited to identify intact old-growth forests habitats worthy of conservation, due to the presence of many poorly known specialist species. Many surrogate schemes suffer from subjectivity and limited solid background data and were developed exclusively based on expert knowledge, sometimes even as proposals to be tested by a broader community (e.g. Zehfuss and Ostrow, 2005). This lack of conceptual clarity and scientific evidence is a weakness, as it hampers evidence-based conservation decisions. The lack of statistical evidence is not unique to fungi, but is a problem for biodiversity surrogates in many organism groups (Gao et al., 2015).

The first substantial critique of the use of indicator species to assess local stand continuity in forests was posed by Nordén and Appelqvist (2001) and Rolstad et al. (2002). The critique did not only point to the lack of evidence in previously proposed indicator schemes, but also pointed out that the concept of forest continuity is complex, and not always well defined. For instance it is often difficult, or even impossible to distinguish continuity per se from habitat quality, because many old-growth forest microhabitats such as veteran trees take centuries to develop and hence are missing from younger or managed forests. Nordén and Appelqvist (2001) thus noted that saproxylic fungi, being generally well dispersed by tiny, wind borne spores, are likely to depend more on a rich supply of high quality dead wood, than on local forest continuity. If true, a careful recording of dead wood amounts, quality and variation would provide a very good proxy of fungal conservation values, without a need for a specialist-based recording of fungal indicator species (cf. Sætersdal et al., 2004; Similä et al., 2006). However, evidence so far indicates that local dead wood volume is only a moderately good indicator of fungal biodiversity and conservation value (e.g. Christensen et al., 2004; Lassauce et al., 2011; Gao et al., 2015).

Already in the early days of research on old-growth forest fungi some researchers were aware of the need to investigate the scientific evidence behind fungal surrogates. In a classic study, Bader et al. (1995) showed that many polypore species, including several suggested indicator species, were more or less restricted to the least disturbed forest stands with high dead wood amount, while forest stands heavily influenced by forestry hosted only subsets of the species present in the more intact localities. This finding lead to a number of studies exploring the biodiversity indicator potential of fungi based on species richness patterns across sets of study sites. One approach focused on nested subset patterns in fungal communities across management or fragmentation gradients, based on the idea that species with a relative high position in the nested hierarchy are good indicators of species rich communities within or between species groups, if a nested metacommunity structure is prominent (e.g. Kerr et al., 2000). Jonsson and Jonsell (1999) found that polypores were not strong indicators of species richness in other groups across a management gradient while Berglund and Jonsson (2003) reported clear nested patterns of wood-inhabiting fungi within a network of forest habitat patches, proposing that some species could be selected as indicators of species rich polypore communities. However, Sætersdal et al. (2005) found that nested patterns in polypore communities tended to vanish on larger geographical scales, questioning the species-to-species indicator power outside the local region. More recently, Jeppesen and Frøslev (2011) used a variant of the nested subset approach to suggest specific species indicative of species-rich ectomycorrhizal

Cortinarius subg. *Phlegmacium* communities in Danish forests, but so far without testing in other regions.

Other studies expanded the perspective and analyzed the potential of fungi as indicators of species richness in other species groups. In boreal Fennoscandia, at least 11 studies have analyzed the relationship between polypore species richness and the biodiversity of some other species group(s) (reviewed by Junninen and Komonen, 2011). Several studies have also been conducted *vice versa*, i.e. to test if other groups could be used as indicators of fungal diversity (Sætersdal et al., 2004; Chiaruzzi et al., 2005; McMullan-Fisher et al., 2010; Hofmeister et al., 2014; Burgas et al., 2016), typically with an argument that biodiversity indication based on plants or birds is more straightforward than a time-consuming monitoring of macrofungi, involving fungal experts. Most of these studies have analyzed species richness covariance, but some have also, or exclusively, focused on the principle of complementarity that is generally accepted as the most effective approach to maximize species representation within a network of conservation areas (Pressey et al., 1993; Kukkala and Moilanen, 2013). These studies have yielded quite mixed and inconclusive results, which can be summarized by saying that shared richness patterns between fungi and other organisms exist in some, but far from all, conditions and comparisons (Gao et al., 2015).

It is important to note that the general lack of consistency in species richness covariation between fungi and other taxa has mixed implications depending on how indicators are used. In monitoring of local species richness, e.g. in site monitoring, lack of consistency simply implies that fungal indicators are unsuited as surrogates for other organism groups more difficult to monitor. In conservation planning, lack of consistency in richness patterns between fungi and other organisms means that fungi need to be considered explicitly in order to be covered sufficiently, e.g. in selection of reserve networks based on complementarity (e.g. Virolainen et al., 2000).

Other studies have taken an ecological approach, and have investigated the links between potential fungal surrogates and different habitat factors supposed to be important for the conservation of threatened forest biodiversity in general, i.e. assessing fungi as potential umbrellas or focal species, often without stating this explicitly. These studies have analyzed the effects of silvicultural management intensity (Müller et al., 2007), variety of woody debris (Abrego and Salcedo, 2013) and forest fragmentation (Sverdrup-Thygeson and Lindenmayer, 2003; Penttilä et al., 2006; Nordén et al., 2013; Abrego et al., 2015). They have increased our understanding of the ecology of wood-inhabiting fungi, and have generally shown that habitat abundance, habitat quality and forest fragmentation influence fungal communities in complex ways, and have confirmed that some of the older indicator schemes purely based on expert opinion make sense as tools to identify sites minimally influenced by fragmentation and timber extraction (e.g. Penttilä et al., 2006; Nordén et al., 2007; Abrego et al., 2015).

Finally, some studies have focused on fungi as keystone or engineering species, important for creation of old-growth forest habitats, supporting other threatened species, e.g. cavity nesting vertebrates (Cockle et al., 2012; Müller et al., 2014; Löhmus, 2016), epiphytes (Fritz and Heilmann-Clausen, 2010) or saproxylic insects (Komonen, 2003). Even if most of these studies do not directly point to specific fungal species as indicators of conservation value at site level, they often have a considerable educational potential by highlighting the key roles fungi play in saproxylic food webs, and in the creation of habitats for more well-known species, including woodpeckers (cf. Löhmus, 2016).

Many proposed fungal indicators could be criticized for poor, or lacking treatment of, spatial coverage and potential extrapolation. In general, the proper function of an indicator scheme requires that

the proposed connection between the indicator and the target elements remains constant throughout the whole area where it is proposed to be used (Hess et al., 2006). Indicator species are typically originally proposed for a certain area based on field experience from that area. Extrapolation to a wider area is risky and should be discouraged because the original indicator power may, for example, be related to microhabitat conditions etc. making the species' habitat requirements more or less different in the neighbouring area (Hess et al., 2006; Halme et al., 2009a; Holec et al., 2015b). For example, the polypore species suggested in Finland (Kotiranta and Niemelä, 1996) and Sweden (Hallingbäck and Aronson, 2004) to indicate old-growth forest conditions were proposed as a tool for a similar purpose in Corsican pine forests, although no local ecological knowledge was used and no correlations were detected between stand conditions and the presence of the listed species (Norstedt et al., 2001).

Only a few studies have directly investigated the spatial consistency of proposed fungal indicator species but, as mentioned above, Sætersdal et al. (2005) found that nested subset patterns among polypores in Norway were inconsistent over larger spatial scales. In some cases inconsistent patterns in habitat selection between different regions or habitats for suggested indicator species have inspired further taxonomic research. For example, *Antrodia crassa*, considered to be a strong indicator of Pine-dominated virgin forests with long dead wood continuity in Finland (Kotiranta and Niemelä, 1996), proved to circumscribe two species with partially overlapping distribution (Runnel et al., 2014; Spirin et al., 2015) and different habitat and substrate preferences, based on field data from Estonia. In such cases, the indicator value is uncertain until the ecologies and distribution limits are determined.

In summary, the use of fungal surrogate species has moved from an early time of quite free and eager application of experience-based species lists, sometimes backed by rather simple mathematical tests of species co-occurrence patterns, to a time with testing and partial approval of more complex links between habitat quality, landscape history (e.g. fragmentation), fungal biodiversity and indicator values. However, fungal surrogates are still often mentioned, and even applied, in professional conservation planning without clear evidence for their indicator value with respect to defined conservation goals. In some cases it seems that the habitat variables to be indicated (e.g. rich presence of huge fallen trees) are so obvious that an indicator is actually useless. For example, the proposal of a fungal species simply to indicate the presence of large trees would be strictly speaking senseless. However, a species that is tightly connected to veteran trees or other very well defined habitat variables can still be a useful conservation tool even though one surely discovers the tree before the fungus. It may be justified to promote it as a flagship species (Caro, 2010), reflecting the importance of old trees for biodiversity, and because many amateur naturalists find it more interesting to hunt peculiar species with an interesting ecology or amazing morphology, rather than reporting large or old trees.

4. A roadmap towards better protocols for using fungi as biodiversity surrogates in forest ecosystems

Regardless of all the issues related to biodiversity surrogates outlined above, they are commonly used planning and communication tools in practical forest conservation, and it is probable that they will continue to be used in the future. Thus, the conservation community should work for better surrogate systems. Considering the weaknesses of the earlier proposed schemes and conceptual aspects, and practical applicability we here propose a stepwise protocol for evidence-based surrogates selection and use. Our protocol follows and builds on general guidelines suggested for

indicator species selection (Carignan and Villard, 2002; Fleishman et al., 2005; Sætersdal et al., 2005; Halme et al., 2009a, 2009b) but we have adjusted the protocol to focus strictly on fungi in forest ecosystems.

Step 1. Define why do you need a surrogate and for what

Biodiversity surrogates are practical (not primarily scientific) tools. As the first step you have to clarify if and why you need them, and for what purpose, and this purpose should be explicitly stated. There are two main reasons why biodiversity surrogates may be needed, and where fungi have true potential:

- 1) Complexity issue needs to be overcome, i.e. comprehensive biodiversity data is missing, and cost-effective proxies are needed. In this context some species may potentially act as surrogates, which should *simplify* the evaluation of biodiversity and related complex ecological relations in particular habitats, mostly for purposes of nature conservation.
- 2) Awareness needs to be raised or citizens involved with respect to an otherwise overlooked conservation issue. In this context, especially iconic fungal species (having large and beautiful fruit bodies or a special relation to the area studied) with a distinct ecology can be used as a communication tool, to draw attention and assist in telling attractive biodiversity stories, i.e. as flagship species (Caro, 2010).

Step 2. Select surrogate candidates that are easy to record and identify

To be easy to record, surrogates should have long-lasting fruit bodies or at least a long fruiting season (Halme and Kotiaho, 2012; Abrego et al., 2016, 2017; Purhonen et al., 2017). Polypores and stromatic pyrenomycetes are ideal as they fruit for a substantial part of season. Among fungi with ephemeral fruit bodies, species with large, typically abundant or sequentially appearing fruit bodies are easier to find. However, proper data on the relationship between fruit body traits and detectability are scarce (but see Löhmus, 2009). Moreover, to be easy to find, the surrogates should produce fruit bodies each season. Species producing fruit bodies very sporadically should be omitted. Potentially already in the near future DNA methods may enable us to identify mycelia in substrate routinely, but so far we are fruit body dependent for extensive stand scale surveys. Moreover, for stand scale evaluation fruit bodies seem to be a useful and cost-effective tool (Runnel et al., 2015).

To be easy to identify, the surrogate species should be taxonomically unproblematic, with clear delimitation and well-known differences from related species. Species with unclear identity should be omitted from the lists because later to-be-solved taxonomy makes the whole proposed scheme questionable. Even if seemingly well-delimited species are selected, they may be subsequently split to two or more similar species with different morphology, ecology and distribution. To ensure a clarification (via revision) in future, the detected surrogate species should be documented by vouchers from each studied region or even site if possible. Taxonomic uncertainty is less problematic in cases where niche conservatism has caused several related species to have very similar niches. This is, for example, true with *Hygrocybe* species, most of which tend to be limited to nutrient poor grassland biotopes (Rald, 1985), and possibly with smaller *Pluteus* species (Nitare, 2000; Ainsworth, 2004) which mainly seem to associate with forests rich in dead wood in advanced stages of decay.

To give reliable information about their environment, the surrogate species should have narrow ecological amplitude with respect to the purpose of the indication. One should be aware that whereas the ecological requirements and the realized niche of the

candidate species may be well-known or easy to verify in a smaller area (region, country), they may vary along the species' distribution range (e.g. preference for substrates, altitude, habitats etc.). Good ecological knowledge of the candidate within its whole range of distribution is essential for proper surrogate selection at the continental scale.

Step 3. Test the predictive power of the surrogate

If it is intended that surrogates are to be used as planning tools in nature conservation e.g. for area selection, their selection should be based on sound scientific data. Selecting suitable data for evaluating the proposed surrogate is challenging. For example, data collected on different spatial scales may induce different challenges for the analyses. Local data sets (one region, one country, one project, one methodology) may suffer from the danger of omitting or overestimating some facts affecting the true indicator power and general usability of the scheme, but are often reliable and repeatable (verified, homogeneously collected). On the other hand, the more extensive data sets (several countries or databases, high number of contributors, different approaches) better reflect the complexity, but are usually based on heterogeneous methods and qualitatively variable in several ways.

Generally, one should test the relation between species' occurrence and the selected environmental variable based on appropriate statistics at the appropriate scale. On large, for example continental scale, the 'indicator power' of most species may be decreased by changing species' preferences or realized niche along the latitude/longitude/altitude gradient. Briefly, the same species often prefers other habitats, substrates etc. in various biogeographic zones (temperate, hemiboreal, boreal etc.), and, thus, cannot be used as a surrogate in the same way for different zones. In this issue, [Abrego et al. \(2016a, 2016b\)](#), present an approach for indicator selection based on comprehensive field data. The study used single species modelling of habitat needs for 105 fungal species across 53 forest sites across Europe and identified five species (*Biscogniauxia nummularia*, *Camarops tubulina*, *Ceriporiopsis gilvescens*, *Flammulaster limulatus*, *Pluteus chrysophaeus*) to be indicative of forest connectivity or reserve size, while other species, most surprisingly *Hericium coralloides* suggested as an indicator of conservation value in several schemes (e.g. [Christensen et al., 2004](#)), were not supported as being significantly associated with this measure of forest integrity. A more specific example is provided by *Pseudorhizina sphaerospora*, a rare and iconic species with large and beautiful fruitbodies, that is known only from virgin forests in the Czech Republic, whereas in Nordic countries it inhabits secondary human-influenced habitats like sawdust piles ([Holec and Beran, 2007](#)).

It is important also to include verified negative data on the occurrence of the surrogate candidate. When evaluating its relation to virgin forests, we also need the information that the species does not occur in the managed ones. In most cases some occurrences are from the 'wrong' habitats and we have to analyze how the unusual occurrences affect the indicator power. For example, [Runnel and Lõhmus \(2017\)](#) showed that a majority of the 'old-growth forest indicators' in Estonia were present in managed forests too. Such a result was possible only through quantitative analysis of an extensive data set covering both virgin and managed sites.

Depending on the aims of the monitoring program, and the level of public involvement, it might be justified to prioritize flagship qualities over strict indicator values. This is especially true in citizen science projects, where iconic species should be included to raise public awareness.

In larger surrogate lists, especially those created for biodiversity and ecosystem integrity evaluation, it is helpful to describe the surrogate type (see Introduction) or add some specifications (e.g.

species preferring natural forests, diagnostic species of the relevant habitat, etc.). It is also possible to assign points to the individual species and count up the total indicator score of the habitat evaluated ([Rotheroe, 2001](#)). Such a simplified approach, although rather arbitrary, fits for comparison of sites having similar size and habitat type and helps to distinguish the most valuable ones. Moreover, it is sometimes required by nature protection authorities and decision makers like foresters or politicians. If so, the grading should be well justified scientifically to prevent erroneous conclusions.

5. Conclusive remarks

The liberal use of the different biodiversity surrogate concepts has to some degree undermined the coherence of the terminology and makes it, even today, somewhat difficult to know for example what 'an indicator species' means in fungal conservation literature and projects. However, the surrogate schemes have played a major role in 1) raising the case of fungi being an important aspect of forest biodiversity; 2) involving amateurs and consultants in recording fungi and their habitats; and 3) stimulating research on the ecology and taxonomy of suggested indicator fungi. In that way they have acted as flagship species, promoting fungal biodiversity research and conservation in general even if this was not the main purpose in suggesting them. Further, they have fueled research in the ecology of forest fungi, and their complex associations with their habitats in space and time. Unfortunately, one of their primary functions – selecting and saving valuable forest sites from deforestation or inappropriate forest management decreasing biodiversity and ecosystem integrity – has so far been used only in some countries, depending on the power of the mycologist's voice, nature protection praxis and political systems. Greater effectivity in using fungal surrogates can be achieved by closer cooperation between mycologists, nature protection authorities, foresters, and politicians ([Heilmann-Clausen et al., 2015](#)).

The future role of fungal biodiversity surrogates is more uncertain. We recommend that further steps are taken to make sure that fungal biodiversity surrogates used in professional monitoring are based on systematically collected datasets and quantitative analyses based on them. Producing such databases with high standards and proper methods often requires collaboration between taxonomists and ecologists or conservation biologists (see [Halme et al., 2015](#); [Sheldon, 2016](#)). However, the use of fungal biodiversity surrogates to raise awareness of threatened fungal habitats with the broader public cannot always be based on strong evidence. At least in Fennoscandia, habitat requirements of wood-inhabiting fungi have been studied for decades and hence allow development of scientifically sound indicator schemes, although the knowledge basis on ectomycorrhizal fungal communities in the same region is much more fragmentary. The same applies for wood-inhabiting fungi in other regions of the world. In such cases, we encourage adopting the flagship species concept more commonly, to raise awareness, and fuel research that will increase the knowledge of fungal biodiversity hotspots and what they need to persist.

We also welcome novel approaches for using fungi in nature management and ecological research based on surrogate approaches. For example, within the frames of the EU habitat directive new fungal indicator schemes are being developed, partly inspired by the total neglect of fungi in the original lists ([Dahlberg et al., 2010](#)). In Denmark a list of 13 wood-inhabiting fungi is already used for the monitoring of conservation status in forested EU habitat types ([Rune et al., 2007](#)), and in the Czech Republic a project is now finishing to develop lists of fungi with the specific aim of evaluating conservational value of habitats (those relevant

for macrofungi, i.e. of terrestrial ecosystems) protected within the Natura 2000 framework. The resulting lists are developed based on expert knowledge, mycological inventories of selected sites and national fungal records' databases. They provide an attempt to grade the indicator value of individual species, also seen in the comprehensive lists of soil living fungal indicator species selected to assess habitat quality in Finnish forest habitats (Bonsdorff et al., 2014).

Even though these developments are so far insufficiently supported by scientific evidence, they underline that fungi are increasingly being taken seriously as tools in habitat assessment and conservation, and it will be interesting to see if they will inspire further ecological research in fungal ecology in the coming decades.

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