The history and future of fungi as biodiversity surrogates in forests

Panu Halme¹, b, *, Jan Holec c, Jacob Heilmann-Clausen d

¹ Jyväskylä University Museum, University of Jyväskylä, Finland
² Department of Biological and Environmental Science, University of Jyväskylä, Finland
³ Mycological Department, National Museum, Cirkusová 1740, Praha 9, Czechia
⁴ Centre for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark

A R T I C L E   I N F O

Article history:
Received 29 April 2016
Received in revised form 9 September 2016
Accepted 14 October 2016
Available online xxx
Corresponding Editor: Claus Bassler

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.

© 2016 Elsevier Ltd and British Mycological Society. All rights reserved.

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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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 spatialation, these proxies, preferably containing data on several different 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
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 (Heiland 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.

<table>
<thead>
<tr>
<th>Title</th>
<th>Reference</th>
<th>Forest type(s)</th>
<th>Scale</th>
<th>No. of Indicators</th>
<th>Groups included</th>
<th>Stated focus</th>
<th>Surrogate concept</th>
<th>Scientific evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood-inhabiting fungi as indicators of nature value in European beech forests</td>
<td>Christensen et al. (2004)</td>
<td>Beech forests</td>
<td>Europe</td>
<td>21</td>
<td>Wood-inhabiting fungi</td>
<td>biotic integrity, conservation value</td>
<td>focal species</td>
<td>Abrego et al. (2015)</td>
</tr>
<tr>
<td>Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe</td>
<td>Odor et al. (2006)</td>
<td>Beech forests</td>
<td>Europe</td>
<td>100</td>
<td>Wood-inhabiting fungi</td>
<td>conservation value (proxy for red-list status)</td>
<td>biodiversity indicator</td>
<td></td>
</tr>
<tr>
<td>Naturnærzeuger – Holzbewohnende Pilze als Indikatoren für Strukturqualität im Wald</td>
<td>Blaschke et al. (2009)</td>
<td>All types of Central European forests</td>
<td>Central Europe</td>
<td>68</td>
<td>Wood-inhabiting fungi</td>
<td>structural quality, nature value</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Hot spots, indicator taxa, complementarity and optimal networks of taiga</td>
<td>Virolainen et al. (2000)</td>
<td>Boreal coniferous forests</td>
<td>Finland</td>
<td>29</td>
<td>Polypores</td>
<td>cross taxon species richness (hot-spot and complementarity)</td>
<td>biodiversity indicator</td>
<td></td>
</tr>
<tr>
<td>Quantifying the indicator power of an indicator species</td>
<td>Halme et al. (2009a)</td>
<td>White-backed woodspecker territories</td>
<td>Finland</td>
<td>5</td>
<td>Polypores</td>
<td>presence of specific red-listed polypores</td>
<td>biodiversity indicator</td>
<td></td>
</tr>
<tr>
<td>Perennial polypores as indicators of annual and red-listed polypores</td>
<td>Halme et al. (2009b)</td>
<td>Boreal forests</td>
<td>Finland</td>
<td>not specified</td>
<td>Polypores</td>
<td>species richness of polypores</td>
<td>biodiversity indicator</td>
<td></td>
</tr>
<tr>
<td>Indicator fungi</td>
<td>Bonsdorff et al. (2014)</td>
<td>15 different boreal forest types</td>
<td>Finland</td>
<td>545</td>
<td>Macrofungi, especially mycorrhizal fungi</td>
<td>Evaluating habitat’s conservation value</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Wood-inhabiting fungi as indicators of continuity in spruce forests in eastern Norway</td>
<td>Bredesen et al. (1997)</td>
<td>Spruce forests</td>
<td>Eastern Norway</td>
<td>6</td>
<td>Wood-inhabiting fungi</td>
<td>Continuity in the presence of dead wood</td>
<td>focal species</td>
<td>Testing of indicator value in paper</td>
</tr>
<tr>
<td>Exploring potential biodiversity indicators in boreal forests</td>
<td>Jonsson and Jonssell (1999)</td>
<td>Boreal spruce forest</td>
<td>Sweden</td>
<td>42</td>
<td>Polypores</td>
<td>cross taxon species richness</td>
<td>biodiversity indicator</td>
<td>Test for nested subset patterns</td>
</tr>
<tr>
<td>Indicator species for assessing the nature conservation value of woodland sites – A flora of selected cryptogams</td>
<td>Vesterholt (1991)</td>
<td>Different boreal forest types</td>
<td>Sweden</td>
<td>139 taxa</td>
<td>Macrofungi, especially mycorrhizal fungi</td>
<td>nature/ conservation value</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Fungi on beech logs - indicators of valuable deciduous forest habitats</td>
<td>Jeppesen and Fraslev (2011)</td>
<td>Beech forests</td>
<td>Denmark</td>
<td>42</td>
<td>Phlegmacium</td>
<td>species richness of Polypores</td>
<td>biodiversity indicator</td>
<td></td>
</tr>
<tr>
<td>Knoldslørhatte som indikatorar ter gennem 20 år</td>
<td>Rune et al. (2007)</td>
<td>Natura 2000 forest habitat types in Denmark</td>
<td>Denmark</td>
<td>13</td>
<td>Wood-inhabiting fungi</td>
<td>conservation status</td>
<td>focal species</td>
<td>Ejrnæs et al. 2009</td>
</tr>
<tr>
<td>25 danske indikator-arter (svampe, moss og laver) til overvågning af skovhabitat-typer (NOVANA).</td>
<td>Parmasto and Parmasto (1997)</td>
<td>Southern Taiga Zone forests (pine, spruce)</td>
<td>Estonia</td>
<td>42</td>
<td>Macrofungi, mostly wood-inhabiting fungi</td>
<td>primeval forest conditions (continuity and lack of disturbance)</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Lignicolous Aphyllorheales of old and primeval forests in Estonia 1</td>
<td>Parmasto (2001)</td>
<td>Homalotrichaceae forest types in Estonia</td>
<td>Estonia</td>
<td>49</td>
<td>Macrofungi, mostly wood-inhabiting fungi</td>
<td>biotic integrity, conservation value</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Fungi as indicators of primeval and old-growth forests deserving protection</td>
<td>Löhmus (2016)</td>
<td>Pine-dominated forests</td>
<td>Estonia</td>
<td>1</td>
<td>Phellinus pini</td>
<td>diversity of cavity-nesting birds</td>
<td>biodiversity indicator</td>
<td></td>
</tr>
<tr>
<td>Habitat indicators for cavity-nesters: The polypore Phellinus pini in pine forests</td>
<td>Ainsworth (2004)</td>
<td>Beech forest</td>
<td>UK</td>
<td>30</td>
<td>Wood-inhabiting fungi</td>
<td>conservation value</td>
<td>focal species</td>
<td></td>
</tr>
</tbody>
</table>

(continued on next page)
Relict fungi of primeval forests in the Świętokrzyskie Mountains (Central Poland)
Luszczyński (2003)
Pine, oak, beech, beech-fir forests
Poland: Świętokrzyskie Mountains
30
Macrofungi
primavle forest conditions
focal species

Characteristic species of important sites for beech-inhabiting fungi in Belgium and The Netherlands
Walleyn and Veerkamp (2005)
Beech forest
Belgium
21
Wood-inhabiting fungi
management intensity
focal species

Mykologischer Vergleich zwischen Naturschutzgebieten und Forstflächen
Nuss (1999)
Montane beech-fir spruce forest
Germany: Bavaria
57
Macrofungi, mostly wood-inhabiting fungi
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

Auf natürliche, vom Menschen nur minimal beeinflusste Vegetation beschränkte Grodipilze
Holec (2003)
Central European montane ecosystems
Czech Rep.: Bohemian Forest
26
Macrofungi, mostly wood-inhabiting fungi
primavle 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 fungi
primavle 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
primavle forest conditions
focal species

### Table 1 (continued)

<table>
<thead>
<tr>
<th>Title</th>
<th>Reference</th>
<th>Forest type(s)</th>
<th>Scale</th>
<th>No. of Indicators</th>
<th>Groups included</th>
<th>Stated focus</th>
<th>Surrogate concept</th>
<th>Scientific evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relict fungi of primeval forests in the Świętokrzyskie Mountains (Central Poland)</td>
<td>Luszczyński (2003)</td>
<td>Pine, oak, beech, beech-fir forests</td>
<td>Poland: Świętokrzyskie Mountains</td>
<td>30</td>
<td>Macrofungi</td>
<td>primavle forest conditions</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Characteristic species of important sites for beech-inhabiting fungi in Belgium and The Netherlands</td>
<td>Walleyn and Veerkamp (2005)</td>
<td>Beech forest</td>
<td>Belgium</td>
<td>21</td>
<td>Wood-inhabiting fungi</td>
<td>management intensity</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Assemblages of wood-inhabiting fungi related to silvicultural management intensity in beech forests in southern Germany</td>
<td>Müller et al. (2007)</td>
<td>Beech forest</td>
<td>Germany: southern part</td>
<td>18</td>
<td>Wood-inhabiting fungi</td>
<td>management intensity</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Auf natürliche, vom Menschen nur minimal beeinflusste Vegetation beschränkte Grodipilze</td>
<td>Holec (2003)</td>
<td>Central European montane ecosystems</td>
<td>Czech Rep.: Bohemian Forest</td>
<td>26</td>
<td>Macrofungi, mostly wood-inhabiting fungi</td>
<td>primavle forest conditions</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>Interesting macrofungi from the Eastern Carpathians, Ukraine and their value as bioindicators of primeval and near-natural forests</td>
<td>Holec (2008)</td>
<td>Montane beech-fir spruce and ravine forests</td>
<td>Ukraine: Eastern Carpathians</td>
<td>10</td>
<td>Macrofungi, mostly wood-inhabiting fungi</td>
<td>primavle forest conditions</td>
<td>focal species</td>
<td></td>
</tr>
<tr>
<td>An attempt to a list of indicator fungi (Aphyllophorales) for old forests of beech and fir in former Yugoslavia</td>
<td>Tortić (1998)</td>
<td>Old and primeval beech-fir-spruce forests</td>
<td>former Yugoslavia</td>
<td>42</td>
<td>Wood-inhabiting fungi</td>
<td>primavle forest conditions</td>
<td>focal species</td>
<td></td>
</tr>
</tbody>
</table>
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 Ostrom, 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 Norden and Appelqvist (2001) and Roistad 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 that many species well defined for instance, as veteran trees take centuries to develop and hence are missing from younger or managed forests. Norden 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 Benglund and Jonsson (2003) reported clear nested patterns of wood-inhabiting fungi within the 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 tend to vanish on larger geographical scales, questioning the species-to-species indicator power outside the local region. More recently, Jeppesen and Froslev (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; Chiarelli 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 combinations (Gao et al., 2015).

It is important to note that the general lack of consistency in species richness correlation 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; Norden 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; Norden 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 ele-
ments remains constant throughout the whole area where it is
proposed to be used (Hess et al., 2006). Indicator species are typi-
cally originally proposed for a certain area based on field experi-
ience 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 ne-
ighbouring area (Hess et al., 2006; Halme et al., 2009a; Holec et al.,
2015b). For example, the polyphore species suggested in Finland
(Kotiranta and Niemelä, 1996) and Sweden (Hallingback 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 correla-
tions 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 con-
spicuity of proposed fungal indicator species but, as mentioned
above, Sætersdal et al. (2005) found that nested subset patterns
among polyphores in Norway were inconsistent over larger spatial
scales. In some cases inconsistent patterns in habitat selection be-
tween different regions or habitats for suggested indicator species
have inspired further taxonomic research. For example, Anotrepa
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 mathe-
atical 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 plan-
ning 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 communi-
cation 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 taxo-
nomically 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 tax-
onomy makes the whole proposed scheme questionable. Even if
seemingly well-delimited species are selected, they may be sub-
sequently 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 bio-
topes (Raid, 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 sur-
rogate 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

Please cite this article in press as: Halme, P., et al., The history and future of fungi as biodiversity surrogates in forests, Fungal Ecology (2016),
http://dx.doi.org/10.1016/j.funeco.2016.10.005
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 gigavescens, Flammulaster limulatus, Plateus 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 effectiveness 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 (Dahlgberg 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 (Runef 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 opportunity 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.

Acknowledgments

We are grateful to attendees of the Fungi of Central European Old-Growth Forests Symposium for fruitful discussion on this topic during the meeting and to Olli Manninen, Sergey Volobuev and Panu Kunttu for valuable comments on the use of indicator species in forest conservation activities in Fennoscandia and western Russia. JH was financially supported by the Ministry of Culture of the Czech Republic (DKRVO 2016/08, National Museum, 00023272) and PH by Kfon foundation.

References


Please cite this article in press as: Halme, P., et al., The history and future of fungi as biodiversity surrogates in forests, Fungal Ecology (2016), http://dx.doi.org/10.1016/j.funeco.2016.10.005