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Fungal targets and tools
for forest conservation

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1. INTRODUCTION

1.1 Forests as fungal habitats

The Fungi constitute a megadiverse kingdom with an estimated minimum of 712 000 species, of which only ca. 11% have been described by science (Schmit & Mueller 2007). Fungi are present virtually everywhere in the environment, but forest is one of their most species-rich habitats. It is, however, not easy to estimate how many fungal species live in forests. Due to their cryptic lifestyle and erratic fruit-body formation, even macrofungal species (fungi visible with the naked eye) in a single forest stand can be missed despite of repeating surveys during several years (Straatsma et al. 2001; Piepenbring et al. 2012). Although new-generation molecular methods allow ecologists to increasingly explore the hidden parts of fungal communities, such research is so-far difficult to translate into formal species names – the taxonomy lags behind the data (Hibbett 2016). One of the few exhaustive studies on the magnitude of fungal species-richness originates from Esher Common in Great Britain. This well-studied 400-ha forest is known to host a striking number of 2900 non-lichenized ascomycetes (Cannon et al. 2001). Fungal species-richness can be astounding even on the scale of one tree. For example, a single European aspen has been shown to host hundreds of species of ectomycorrhizal fungi in Estonia (Bahram et al. 2011) and a single *Elaeocarpus* tree hosted more than 200 ascomycete taxa in Papua New Guinea (Aptroot 2001).

Fungi are not just diverse – they are also key players in forest ecosystems. Major functional groups of forest fungi include the following four. (i) Decomposers of dead wood and leaf litter who recycle nutrients back into production using their enzymes that decompose dead plant tissues (Baldrian 2008). The decomposers have an important role in soil formation and, consequently, for forest ecosystem productivity (Lindahl et al. 2002). (ii) Symbiotic mycorrhizal fungi living in the soil and colonizing plant roots. Their association with plants supplies these fungi with carbohydrates; in return they supply the plants with mineral nutrients, and other useful compounds (Buée et al. 2009). At least in boreal forests, dead mycelia of these fungi store a significant amount of the carbon sequestered in forest soil (Clemmensen et al. 2013). (iii) Tree pathogens, who can affect tree-species composition of forests over large areas, e.g., *Hymenoscyphus fraxineus* colonizing and exploiting the leaves of European ashes (Gross et al. 2014) and *Ophiostoma* spp*.,* infecting the vascular system of elms (Brasier 2000). (iv) Lichens, i.e., fungi living in symbiosis with algae or cyanobacteria (or both). Most forest lichens are epiphytes (attached to trees) and they participate in nutrient cycling, notably in nitrogen fixing (in case of symbiosis with cyanobacteria) (Nash 1996). Lichens have an ability to store large quantities of water, which, in turn, can significantly impact forest hydrology (Pypker et al. 2006). Most fungi (including those described above) participate in forest food webs: there are numerous other organisms feeding on fungal mycelia, spores, fruit-bodies, and lichen thalli. These organisms, further,

have their predators, parasites, parasitoids or commensals whose existence may depend directly upon their host (Stokland et al. 2012). Functional chains of similar complexity are based on the habitat providing function of forest fungi (Stokland et al. 2012). If such chains break (e.g., by local extirpation of a fungal species or group), extinction cascades involving several other organisms may follow (e.g., Komonen et al. 2000).

It is obvious that forest fungi have been affected by the major human induced transformation of their habitats, with consequences on ecosystem functioning. During a few centuries, forests have largely become human-dominated eco-systems (Noble & Dirzo 1997). In addition to direct area loss, human impacts on forests include fragmentation of the landscape, and changes in the structure and composition of the remaining forest patches (FAO 2010). Such changes are presumed to affect all functional groups of forest fungi: some species are decreasing because their habitats are disappearing; others are affected by more complex shifts in the competitive balance forced upon them by forestry (Dahlberg et al. 2010). For instance, forest harvest causes assemblage shifts in ectomycorrhizal fungi towards the dominance of less carbon demanding species, which can be sustained by the young trees in regenerating forests (Durall et al. 2005). However, while the general theory of biodiversity-forest functioning link has been well developed (e.g., Bengtsson et al. 2000), there is surprisingly little data on the specific consequences of fungal assemblage changes and reduced diversity (Jones et al. 2003; Lonsdale et al. 2008; Courty et al. 2010). Such information would offer, besides theoretical interest, a valuable practical input for planning of forest reserves, species conservation and sustainable forest management. Yet, fungi have received relatively little atten-tion by the conservation community (Heilmann-Clausen & Vesterholt 2008).

1.2 Fungi inhabiting dead wood and old living trees as conservation targets...

A major human-induced forest change with a strong negative impact on fungi is the decrease of coarse dead wood and large old trees. In the intensively managed European forest regions, the amount of these forest structures has declined by more than 90% compared to pre-industrial time (Siitonen 2001; Jönsson et al. 2009). Various fungal groups depend on old and dead trees within their life cycle (Stokland et al. 2012) and consequences of their habitat decline have been growingly acknowledged during the past two decades (e.g., Berg et al. 1994; Renvall 1995; Esseen et al. 1996; Molina et al. 2001; Lonsdale et al. 2008; Junninen & Komonen 2011). Two conspicuous groups of such fungi are also studied in the current thesis: polypores, and lichens growing on exposed wood and on old hardwood trees.

My main study objects are polypores, which constitute a polyphyletic group of mostly saprotrophic basidiomycetes. They are traditionally delimited based on morphology – most species have a poroid hymenium. Polypores belong to

the dominant dead-wood decomposers in forests (Boddy & Watkinson 1995), and they are particularly species-rich on downed dead wood (Junninen & Komonen 2011). A part of my thesis also explores lichens – more specifically, I examine epixylic (exposed wood-surface inhabiting) assemblages that are most distinct on decorticated snags (Lõhmus & Lõhmus 2001; 2011), and corticolous species (such as *Lobaria pulmonaria*) that require old trees with specific bark texture and canopy microhabitats (e.g., Kuusinen 1996; McCune et al. 2000). In addition, I have included some lichenicolous and some saprotrophic fungi traditionally surveyed by lichenologists, e.g., calicioid ascomycetes. Common threats to all these ecologically and functionally different fungi are the impoverishment, decline and isolation of their old-forest habitat.

It is not surprising that the assemblages of polypores, corticolous and epixylic lichens are often reported to be substantially poorer in forests managed for timber extraction than in natural old-growth stands (Junninen & Komonen 2011; Nascimbene et al. 2013). Sensitive species can become mostly or entirely restricted to the remaining old-growth fragments (e.g., Nitare 2000; Niemelä 2008), due to the scarcity and reduced quality of substrates in managed forests. Managed forests may lack high-quality substrates such as very large tree individuals, large-diameter logs and snags (Siitonen 2001; Lõhmus & Kraut 2010). For polypores and lichens, the available (usually relatively small) tree-trunks, offer less colonisable space (Renvall 1995, Kruys et al. 1999, Humphrey et al. 2002), poorer choise of microhabitats (Humphrey et al. 2002) and reduced habitat stability both in terms of metapopulation dynamics (increased turnover and extinction rates; Jönsson et al. 2008) and microclimate. For some polypores, small tree-trunks may also not have enough nutrients to enable fruit-body formation (Moore et al. 2008). Silviculture also typically reduces tree species diversity. For example in Scandinavia, deciduous trees have long been actively suppressed (Esseen et al. 1997); and thus are poorly available for numerous specialist fungi in managed forests (Berg et al. 1994). Furthermore, any reduction of structural diversity of forest may eliminate vital combinations of habitat characteristics for highly specialized species, e.g., combinations of sufficient size, tree species, mortality factors, decay phases, microclimatic conditions, etc. (Stokland et al. 2012).

Vulnerability of a species to habitat change also depends on its dispersal ability (Nordén & Appelqvist 2001). Both living trees and dead wood are dynamic habitats, and local (substrate turnover-caused) extinctions and con-current colonisations of new substrates are a part of natural metapopulation dynamics of fungi inhabiting these structures (Jönsson et al. 2008). It is probably an adaptive trait that fungi specialized on ephemeral habitats mostly reproduce with small, highly dispersive spores (Tibell 1994; Spribille et al. 2008; Norros et al. 2014). However, there seem to be large differences between effective colonisation ability among species. Distribution and genetic structure of populations of some (common) species indicates that they are capable of crossing large distances (e.g., Tibell 1994; Högberg et al. 1999; Kauserud & Schumacher 2003), while effective colonisation of several (rare, specialist)

species may be limited already within dozens of meters (Öckinger et al. 2005; Norros et al. 2012). Small effective colonisation distances may explain the absence of some species from appropriate substrates in forests that have lost spatiotemporal connectivity (Sillett et al. 2000; Sverdrup-Thygeson & Linden-mayer 2003; Penttilä et al. 2006; Nordén et al. 2013). Species specific habitat models to describe such limiting factors are, however, still rare and sought after in fungal ecology (Molina et al. 2011; see also Lõhmus 2015).

Understanding whether species are limited by habitat availability or dispersal is fundamental for developing conservation strategies in modern fragmented landscapes. The basic conservation strategies for old-forest fungi include protecting sites with diverse natural forests and specific conservation measures in production forests (Dahlberg et al. 2010). Unfortunately, it is not possible to sustain all forest biodiversity within the small and fragmented area of protected forests in the long term, because the net loss of species would eventually equal the net loss of habitat (Rosenzweig 2003). The isolated populations of poor dispersers inhabiting dead wood and old living trees in small forest set-asides are particularly prone to stochastic extinction (Berglund & Jonsson 2008; Jönsson et al. 2016) and genetic impoverishment (Stenlid & Gustafsson 2001). The most sensitive fungi may never form viable populations outside protected areas, but the prospects for many other species could be increased by creating adequate structures through modified silviculture and habitat restoration. This could also maintain certain ecosystem functions performed by fungi in production forests, the loss of which could have unexpected consequences. To summarize, effective protection of forest species should aim at an appropriate balance between 'land sharing' and 'land sparing' (Franklin & Lindenmayer 2009; but see Edwards et al. 2014).

1.3 ... and as tools in forest conservation and management

In addition to fungi, many other taxon groups form species-rich assemblages in forests. Surveying all that biodiversity, and the related ecosystem processes and qualities is practically impossible. It is thus challenging to answer the questions of where biodiversity is, and how it responds to the changing environment, which are an everyday part of forest policy making and conservation manage-ment. One possible tool in answering these questions could be the use of indicator species or groups. In forest conservation, indicators are most needed for (i) identifying high conservation value forests on the landscape; (ii) monitoring the influences of conservation measures in forest management, i.a. on threatened species; (iii) documenting the effects of global change to biodiversity across ecosystems (Paillet et al. 2013). There are many require-ments for an ideal indicator, and finding effective ones can be difficult (e.g., Dale & Beyeler 2001). However, fungi inhabiting dead wood and old living

trees, particularly conspicuous polypores and lichens, have been both discussed and used for such purpose since the 1990s (e.g., Esseen et al. 1997, and references therein).

One can distinguish between "biodiversity indicators" which are species that indicate the presence of other taxa, and "environmental or ecological indicators" that act as proxies for hidden features or holistic 'health' of the environment (Caro 2010). Certain polypores and lichens could be effective as indicators of other fungal taxa inhabiting the same substrates (as reviewed by Nilsson et al. 2001; Junninen & Komonen 2011; Ellis 2012). Identifying so-called woodland key habitats (stands valuable for threatened species) is the most widely advocated practical example in Europe and several conspicuous non-threatened polypores and epiphytic lichens are used for that (Nitare 2000; Ek et al. 2002; Andersson et al. 2005; Anon. 2010). A general problem with fungal indicators is that most indicator species have been listed based on the expert opinion of field mycologists. Balanced studies verifying that the indicators indicate what they are assumed to indicate are rare (Heilmann-Clausen & Vesterholt 2008; but see also Nordén et al. 2007). Other proposed approaches include the use of species-richness. For example, polypores with long-living fruit-bodies could explain the variation of annuals (Halme et al. 2009), and polypores in general could also represent the less detectable corticoid fungi (Berglund & Jonsson 2001). Yet, species-richness alone can be misleading, because threatened fungal assemblages are not necessarily species-rich (Heilmann-Clausen & Vesterholt 2008), and the estimates of species-richness are prone to bias. Furthermore, confirming a general pattern (Westgate et al. 2014), spatial diversity patterns of polypores and lichens are typically not congruent with more distant taxon groups (e.g., Jonsson & Jonsell 1999; Berglund & Jonsson 2001; Sætersdal et al. 2005; Similä et al. 2006).

Polypores and lichens could also act as proxies for some hidden habitat properties and ecosystem processes, including "early warnings" of mal-functioning. (i) In terms of hidden habitat properties, lichens have served as one of the earliest examples of environmental indicators: already in the 19th century, these fungi were proposed to signal changes in air quality (Conti & Cecchetti 2001). As another well-known example, both polypores and lichens have been suggested to indicate ecological continuity in boreal and temperate forests, meaning that a forest has existed in a particular place for a long time (Rose 1976; Esseen et al. 1997). The concept of ecological continuity has been, however, premature for universal use, lacking both theoretical and practical evidence (Nordén & Appelqvist 2001; Rolstad et al. 2002) and, at least on a stand scale, continuity may be easier to measure directly from the environ-mental conditions (Lindenmayer & Likens 2011). Other, mostly theoretical indicator targets include certain wood properties (e.g., the occurrence of *Fomi-topsis rosea* on dense, slowly grown wood; Edman et al. 2006) and micro-climatic fluctuations in a habitat (e.g. for temporal exposure to heat that favours specific species; Carlsson et al. 2014). (ii) Dispersal over landscapes is an example of a hidden ecosystem process: the proposed indicators for this include

some conspicuous corticolous lichens (notably *Lobaria pulmonaria*; e.g., Öckinger et al. 2005) and wood-decayers sensitive to habitat fragmentation (e.g., Norros et al. 2012). A less discussed, but obvious, potential is to use fruit-bodies of certain polypores as indicators of decay processes of high ecological importance. For example, fruit-bodies of *Phellinus* spp. can appear on trees long before the heart-rot allows the formation of tree cavities (Lõhmus 2016).

1.4 Motivation and aims

The general aim of my thesis is to assess and develop the conservation practices, which are based on the ecology of fungi inhabiting dead wood and old living trees. Such practices include forest protection, biodiversity measures in forest management, and monitoring. My starting point is that there is a necessity to broaden the existing approaches both methodologically and by considering a wider range of environmental conditions. Regarding methodology, I address two major pragmatic approaches in fungal conservation: fruit-body sampling for compiling species lists in the field, and the use of fungal indicators for detecting valuable old-forest habitats. The latter form a direct link with forest-protection issues, which have been mostly studied in high-contrast landscapes, where old-growth remnants are embedded in intensively managed matrix (e.g., Esseen et al. 1997; Siitonen 2001; Penttilä et al. 2004). I contribute with studies from Estonia where dead wood is relatively abundant throughout the forest landscape. Such conditions enable to distinguish the influences of old-forest loss, habitat fragmentation, and intensive management at the stand scale. The Estonian system has been called a "medium-intensity semi-natural forestry approach" (Lõhmus et al. 2016). Through the treatment of old-forest associations of fungi in such lower-contrast landscapes, I reach the issue of how to combine protected and production forests for fungal conservation.

Correspondingly, my three specific objectives in this thesis are:
(i)   To assess scale-dependence of the bias of fruit-body surveys that describe fungal assemblages on a species level (study **I**), and to validate the field methods used in studies **II** and **III**. The hypothesis is that fruit-body based species lists may be incomplete at the tree scale (e.g., Boddy 2001; Halme & Kotiaho 2012) but the lists become increasingly reliable in larger sampling units.
(ii) To explore the old-forest associations and indicator value of polypore species. In study **II**, I investigate a broad hypothesis that, due to relatively good substrate connectivity, old-forest associations are weak and can largely be explained by variation of substrate amounts in Estonian forests. Studies **III–IV** focus on a specific old-forest species, *Antrodia crassa*. These studies exemplify the importance of proper study designs and high-resolution molecular identification for detecting cryptic species (cf.

Bickford et al. 2007) and for allowing sound assessments of fungal habitat and indicator value.

(iii) To describe major habitat qualities for fungi in the Estonian forest landscapes. Study **II** describes polypore assemblages and their habitat determinants at the stand scale. Study **V** assesses, which characteristics and combinations of retention trees provide best habitat value for wood-inhabiting fungi. The case study **VI** describes local extinction risk of corticolous lichens due to forest dieback, and discusses this in terms of silviculture.

2. MATERIALS AND METHODS

2.1 Study area and design

The research was carried out in the Estonian mainland (Fig. 1). Estonia is situated in the hemiboreal vegetation zone in Europe (Ahti et al. 1968). The mean air temperature is 17 °C in July and –6 °C in January. The average precipitation is 600–700 mm/yr. The topography is mostly of glacial origin: the dominating landforms are flat and undulating moraine plains and glaciolacustrine plains with abundant clayey deposits and extensive postglacial paludification. Only two study sites were situated >100 m above sea level.

Estonian forest lands (over 2.2 million ha; 51% of the country) do not contain intensive plantations; >90% of forest area is naturally regenerated; and thinning intensity is low. However, because of a long history of clear-cutting, old stands are rare (2% exceed 120 years age; Raudsaar et al. 2014). Typical cut blocks in production forests are small (<5 ha), and since the late 1990s ca. 5% of growing stock is being left as solitary retention trees at harvest (Rosenvald et al. 2008). Ten percent of all forest area is now strictly protected and 15% is managed for environmental values (Raudsaar et al. 2014). Additionally, the state-owned production forests (23%) are managed in compliance with the Forest Stewardship Council (FSC) criteria of sustainable forestry since 2002 (Hain & Ahas 2007).

The studies were conducted in forests that represent five common 'forest types' (site-type groups sensu Lõhmus 1984): (i) dry boreal forests (*Vaccinium myrtillus* and *V. vitis-idaea*-type) on higher fluvioglacial landforms and till mounds with Podzols (pH_{KCl} 3.5–5.0) where the top layer is periodically dry and ground water deeper than 2 m; (ii) meso-eutrophic forests (*Oxalis*- and *Hepatica*-type) on till mounds or rolling plains with Podzols or Stagnic Luvisols (pH_{KCl} 3.2–4.2) where ground water is usually deeper than 2 m; (iii) eutrophic boreo-nemoral and paludifying forests (mostly *Aegopodium* and *Filipendula* types) predominantly on undulating sandy till plains with favorably moist (in springtime anaerobic) Gleyic Gambisols or Luvisols (pH_{KCl} 4.7–6.5) and almost no organic horizon; (iv) mobile-water swamp forests on thin seasonally flooded Eutric Histosols and Fluvisols, with a peat layer ≥30 cm (pH_{KCl} 5.0–6.5) in lowlands and valleys along rivers or around bogs; (v) drained mixotrophic peatland forests (*Oxalis* or *Vaccinium myrtillus* type), which have developed on pine wetlands after at least three decades since ditching. The dry boreal and most drained stands were dominated by Scots pine (*Pinus sylvestris*); the remaining sites hosted conifer/deciduous mixtures with Norway spruce (*Picea abies*) or, in some *Oxalis*-type stands, with Scots pine.
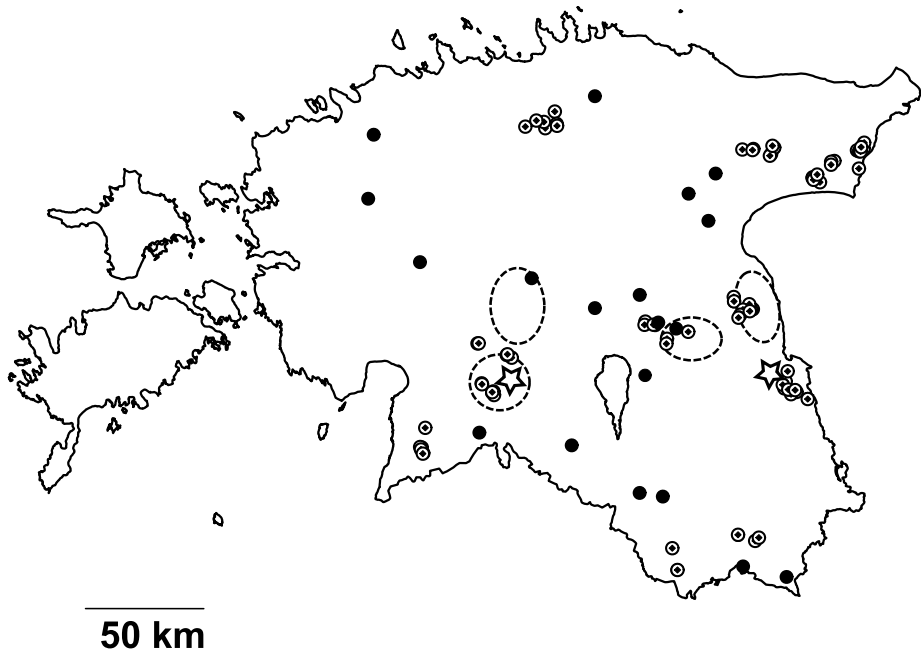
Fig. 1. Locations of the study areas and study sites. Hollow circles are the 92 plots of the balanced design of four management stages (**II–III**); filled circles are the 20 supplementary plots of study **II**. Stars denote the locations of studies **I** (left) and **VI** (right), and ovals delineate the four regions of retention-cut monitoring (**V**).

The studies explored fungal habitat relationships at substrate and forest-stand scales:
1. Study **I** explored 30 fallen tree-trunks for polypore detection bias by comparing molecular records with fruit-body records on the same and adjacent trees. Study **V** described fungal assemblages on 94 snags and 128 fallen trunks (including 73 pairs of snags and trunks created by stem breakages), which were created by dated death of live retention trees on 43 harvested areas. Additionally, 15 snags that had remained from the pre-cut forest and were still standing the ten years post-harvesting were sampled. Study **VI** monitored corticolous lichen populations in a ca. 100 year-old forest-remnant in Eastern Estonia: the question was how the tree-scale extirpations, caused by sudden dieback of their main host tree (*Fraxinus excelsior*), were buffered by alternative host trees.
2. Studies **II** and **III** (supplemented by **IV**) were primarily based on a block design of 92 stands, which were surveyed for full polypore assemblages. The stands represented four forest types (no. 1–4 above) and four management stages: old growth, mature managed forest, and clear-cut with and without retention trees (for other studies on the same design, see, e.g., Lõhmus & Lõhmus 2011; Remm & Lõhmus 2016). Study **II** additionally included 20

15

forest stands to improve polypore habitat modelling with unmanaged forests of four site types (no. 2–5 above) and a range of stand ages.

Study **II** considered also landscape factors (connectivity of forest area and old forests within 1 km) for explaining stand scale abundance of old-forest indicator polypores.

2.2 Field surveys

In the tree-scale surveys, polypores (**I**), lichens (**VI**) or both (**V**) were sampled and the tree trunks surveyed were described (e.g., diameter, decay stage, bark cover %). In study **I**, wood samples were obtained for molecular analyses using an electric drill (five radial holes per fallen trunk), and the same trees were inspected for polypore fruit-bodies in November 2013. In study **V**, epixylic lichens were recorded on exposed wood surfaces of snags (at 0.2–1.8 m height), and polypore fruit-bodies were recorded both on the same snags and fallen trunks (including branches). The polypore survey was repeated in two subsequent autumns to capture species that might skip one year in fruit-body formation. The fieldwork in study **VI** included mapping and monitoring of actual and potential host trees (particularly large ashes, including fallen trees) of *Lobaria pulmonaria* and four other lichenized fungal species of conservation concern in 2009–2013. The lichens were monitored throughout the forest, including detailed mapping of individual thalli of *L. pulmonaria*. For the ash dieback monitoring, the mid-summer condition of a random subsample of 99 live ash trees were recorded annually, using visual estimates of branch mortality and defoliation.

The stand-scale sampling of polypores (**II–III**, also the background survey in **I**) followed a standard rapid survey protocol, which is in use for several plant and fungal groups in Estonia (e.g., Lõhmus & Lõhmus, 2011; Remm et al. 2013). Fruit-bodies of all polypore species (including dead fruit-bodies of annual species) were searched for in 2-ha plots during 4 hours by one person (A. Lõhmus or K. Runnel). The estimates of species abundance were based on the number of 'records'; one record referring to all fruit-bodies of the same species on one substrate item (standing or fallen trunk, fallen branch, rootplate of a fallen tree). For each species in each plot, the first ten records were described in detail (tree species; diameter; decay stage). The abundance of each species was additionally categorized on an approximately logarithmic five-point scale: one record (1), 2–5 records (2), 6–15 records (3), 16–100 records (4) or more than 100 records (5). Up to 150 distinct records per plot could be described within the 4 h.

In the same 2-ha plots, stand structure was measured as described in detail by Lõhmus and Kraut (2010). In each plot, four straight 50-m transects were spaced out, to represent its whole area (in structurally poor dry forests, 1–2 transect lines were added in order to increase the sample size). Two sampling techniques were combined: (i) strip transects for area-based estimation of the

density of live trees, standing dead trees and snags (height at least 1.3 m; diameter ≥10 cm at breast height); (ii) line-intersect method for volumes of downed dead wood (CWD: ≥10 cm in diameter at intersections with the line; fine woody debris, FWD: 0.3–9.9 cm at six 1-m sections established at 10-m intervals). For the purposes of studies **I**, **II** and **III**, plot-scale mean estimates of stand characteristics, considered to be of importance to polypores were used: total volumes of downed FWD and CWD; CWD volumes by tree species and size (e.g., volume of spruce logs at least 30 cm in diameter); and substrate diversity measures (Shannon indices of species diversity and decay-stage diversity of CWD).

The lichen and polypore specimens that could not be reliably identified in the field were collected and identified microscopically. By necessity, the identifications were also checked by sequencing barcode markers of fungi (Section 2.3). For morphological and molecular references, particularly in the taxonomic studies **III** and **IV**, the type specimens and other collections from different fungaria were studied and sequenced.

2.3 Molecular analyses and bioinformatics

I used Illumina MiSeq sequencing for detecting the polypore species present in dead wood as a mycelium (**I**), and Sanger sequencing of fruit-bodies for various purposes – identifying difficult (sterile, juvenile) specimens; confirming crucial morphology-based identifications (**II, III, V**); and conducting phylogenetic analyses (**III, IV**).

'Illumina MiSeq sequencing' refers to the Illumina massively parallel sequencing platform, which is a high-throughput "sequencing-by-synthesis" technology that uses reversible dye terminators for immobilized DNA mole-cules on a solid-state surface (details: **I**). The sawdust from the five drill holes of each trunk was pooled (200 mg of sawdust from each hole) and subsequently grounded in liquid nitrogen. DNA was extracted from approximately 110 mg of the mixed sawdust from each trunk. ITS2 region was amplified for identifi-cation of fungal species. The sequencing was done at the Estonian Genome Center (Tartu, Estonia). The following bioinformatics: (i) distinguished high quality sequence reads; (ii) clustered these into operational taxonomic units (OTUs) at 97% similarity threshold; and (iii) ran BLASTn searches against sequences available public databases to identify the OTUs at best possible taxonomic resolution (97%, 90%, 85%, 80%, and 75% sequence identity criteria used for assigning species, genus, family, order or class names, respectively). All OTUs matching known polypore species and those potentially representing polypores (as judged by the genus or family name) were investigated manually: the closest matches were checked for possible inconsistencies and, if necessary, additional BLAST searches were performed against authors' personal sequence database.

For Sanger sequencing, DNA was extracted from dried fruit-bodies. The nuclear internal transcribed spacer (ITS) and large subunit (LSU) rDNA, and translation elongation factor 1-α (*tef1*; only in **IV**) regions were sequenced (details: **III** and **IV**). The sequences were edited and assembled in Sequencher 5.1 (Gene Codes, Ann Arbor, MI, USA).

2.4 Data processing

In study **I**, the main analyses were based on "molecularly detected" taxa, defined as those OTUs that were represented by at least five sequences in a sample. From each molecularly detected polypore record (identified to species) the distance to the closest fruit-body was measured in GIS, based on field records (0 m for fruit-bodies on the same trunk). Conventional statistics were used for comparing those distances or the species-richness of different trunks: Mann-Whitney U-test, Pearson correlation and simple General Linear Models (GLM).

The main questions addressed in studies **II** and **V** were related to explaining differences in the fungal biota of different types of trees or habitats. For analyzing and illustrating assemblage differences, Multi-Response Permutation Procedures (MRPP) and non-metric multidimensional scaling (NMS) with Sørensen distance as the measure of dissimilarity were used in PC-ORD 6.07 package (McCune & Mefford 2011). The main sources of compositional variation were inferred from correlations between the main ordination axes and habitat (plot or tree) characteristics. The effects of habitat characteristics on fungal species-richness were described using GLM or Generalized Linear Models (GLZ) in STATISTICA 8 software (StatSoft, Inc. 2007). The exact approach and variable transformations were selected based on variable distributions and collinearity.

In study **II**, polypore assemblage composition, species-richness and abundance of specific species were related to habitat characteristics in old growth, mature managed forests, and harvested stands; the main attention was paid on the contrast between old-growth and mature stands. The importance of substrate availability on species-richness was assessed in two stages. First, a full model incorporating forest type and volumes of downed CWD and FWD was built. Then, the additional effect of management stage to this model was checked. 'Old-forest species' were distinguished by analysing the numbers of polypore records by management stages (using Indicator Species Analyses; Dufrêne & Legendre 1997) and in relation to stand age (Spearman's or Pearson's correlation). For each identified old-forest species, habitat models were constructed according to a standard procedure: after idenfitying the best subsets of substrate and habitat factors, the importance of stand age and forest connectivity was checked by adding those variables to the models.

In study **V**, fungal species-richness and assemblage composition (develop-ment) were explored in relation to the characteristics of dead retention trees and

the time since the tree death. For the tree scale species-richness, GLM or GLZ models including significant tree-trunk characteristics were compiled by manually eliminating non-significant factors. Sets of substrate types that would cost-effectively provide habitat for most species at the landscape scale were identified using set-covering approach based on tree species, size (diameter), and substrate type. The null hypothesis was that managers should retain different kinds of trees in approximately equal proportions, because tree species differ in their fungal assemblages and tree deaths are poorly predictable. The set-covering analysis was separately performed for (i) all species recorded; (ii) regularly occurring species (at least three records); (iii) species of conservation concern.

In studies **III** and **IV**, phylogenetic analyses were conducted to explore the identity of specimens similar to *Antrodia crassa*, a putative old-forest polypore that was repeatedly recorded in Estonian cutovers. In addition to sequencing the fruit-bodies collected during the original surveys (study **II**), herbarium specimens and relevant references in public databases were also included. The datasets were aligned with Mafft 7 online version (Katoh & Toh 2008) and edited manually using GeneDoc 2.6.0.3. Bayesian Inference (**III** and **IV**) and Maximum Likelihood (**IV**) phylogenetic analyses were conducted using MrBayes v.3.2.1 (Ronquist et al. 2012) and RAxML-HPC BlackBox 8.0.9 (Stamatakis 2014), respectively. All phylogenetic analyses were run at the CIPRES Science Gateway (Miller et al. 2010).

Study **VI** described the dynamics of *Lobaria pulmonaria* colonies on host trees, including its disappearance on dead/dying ash trees. The approximate colonisation times were estimated for small thalli, considering 2 mm diameter as the starting point and up to 5 mm annual radial growth thereafter (details: **VI**). For describing extirpations, the proportion of thalli lost annually was calculated for every dead host tree. Since late-successional *Ulmus* trees of the subcanopy appeared to be the main alternative hosts, bivariate logistic regression was used to relate their colonisation by tree diameter and the number of *L. pulmonaria* 'source trees' within a 30 m radius.

3. RESULTS

3.1 Polypore fruit-bodies in relation to molecular records (I)

Multiple fruit-body inventories revealed a species pool of 87 polypore species in the studied 70-km^2 landscape. Sixty species were found in the surroundings of the five molecular sampling sites (31–36 species per site; **I**: Table 1). The molecular samples from 30 fallen trees provided 110 records of 14 polypore species (threshold for inclusion at least three sequence reads per sample) or 70 records of 13 species (threshold of at least five sequences). Among the latter, 75% were present as conspecific fruit-bodies within 30 m, including 24% on the same tree (median 15 m, quartile range 2–30 m; n = 70). The proportion of species not found within 100 m was only 6% in the case of the higher inclusion threshold (Fig. 2).
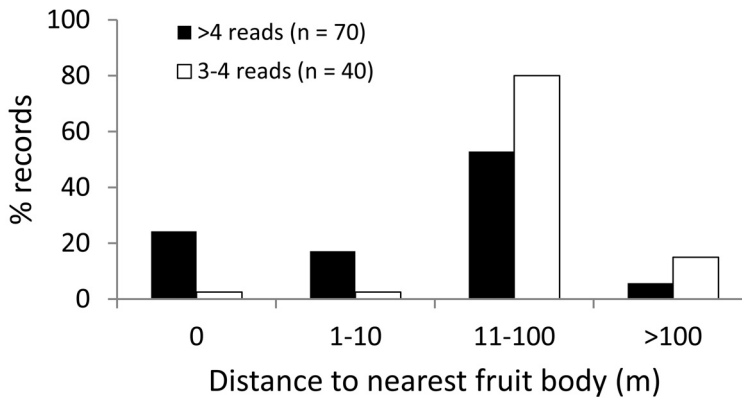

Fig. 2. Distribution of distances to the nearest polypore fruit-body from the molecular records based on at least five versus 3–4 reads (**I**). Difference between the two samples is highly significant (Mann-Whitney U-test: U = 749.5, Z = –4.0, P < 0.001).

3.2 Old-forest associations in polypores (II–IV)

In total, 84 out of ca. 240 Estonian polypore species have been listed as old-forest associated in the references provided in study **II** (Supplement 1). Forty-eight such species were found from the 92 2-ha plots of the main dataset, and 39 species were abundant enough for further analyses. Most of these 39 species occurred in mixedwood sites and did not show a significant preference for old growth (Fig. 3AB; **II**). In particular, managed forests appeared to provide habitats for most of the putative old-forest polypores that inhabit deciduous wood. Several of these species also inhabited harvested areas and belonged to a

group preferring well-decayed, mostly deciduous wood in moist conditions. In the ordination space, the centroids of such species appeared in-between the management-stage polygons (Fig. 3A).

Only ten polypore species showed a statistically significant association with old-growth plots (**II**). Five of these were spruce-inhabiting species whose abundance was influenced by the availability of their particular substrate fraction: large living spruces for *Phellinus chrysoloma*, high total volume of spruce CWD for *Pycnoporellus fulgens* and *Phellinus nigrolimitatus*, and downed trunks at least 20 cm in diameter for *Fomitopsis rosea* and *Junghuhnia collabens*. Only one pine-inhabiting species (the live-tree pathogen *Phellinus pini*) had significant indicator value for old growth – its occurrence depended on the age and abundance of live pines. Landscape connectivity contributed to the substrate availability based models in only two old-forest species: *Fomitopsis rosea* (total forest cover within 1 km) and *Rigidoporus corticola* (share of ≥100 year-old stands within 1 km). The latter was also the only old-forest species for which the age of the sampled stand had a significant independent impact beyond substrate and landscape effects.

The fruit-body surveys in the 92 plots provided five specimens that were initially identified as *Antrodia crassa* – a species that is mostly known to inhabit pines and is used as an old-forest indicator in Northern Europe. All these collections were, however, from unexpected habitats: spruce logs and stumps in clear-cut areas. In the analyses of ITS, LSU rDNA and *tef1* sequences, these specimens formed a distinct lineage closely related to *A. crassa,* described as *A. cretacea* sp. nova (**III, IV**; Fig. 4). The study of herbarium specimens showed that *A. cretacea* is widely distributed in temperate and boreal zones and inhabits several tree species and forest successional stages. In contrast, *A. crassa* is restricted to *Pinus* spp. in deadwood-rich mid- to late-successional forests in the Eurasian boreal zone. Furthermore, four more cryptic species were discovered among the close relatives of *A. crassa* (**IV**). These include one old-forest species, *Antrodia piceata*, which was previously considered conspecific with *Antrodia sitchensis* – a species originally described in the USA. The analyses showed that the European specimens are distinct from those from North-America, and the latter include an additional cryptic species, *A. ignobilis* sp. nova, with a similar morphology but different ecology.
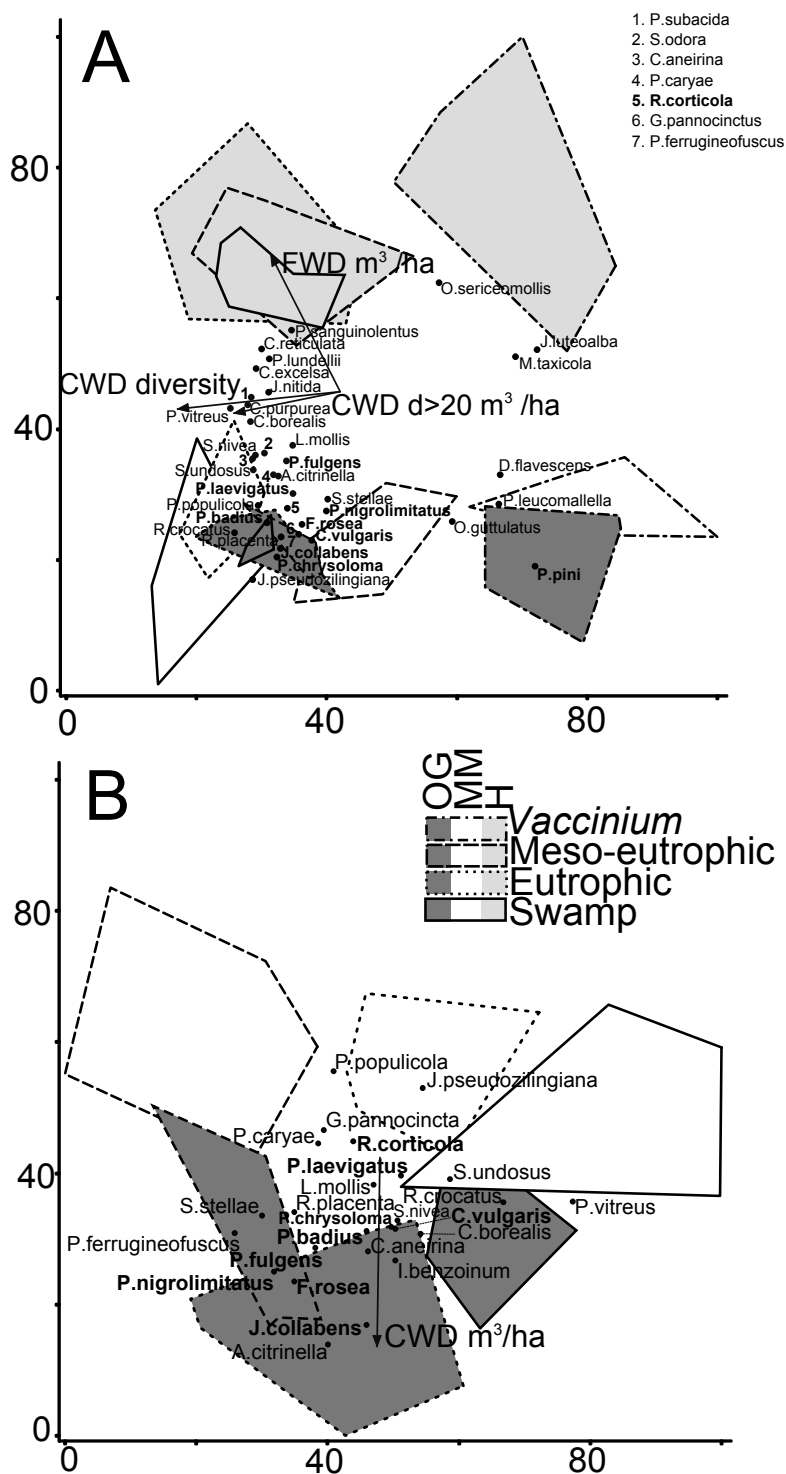
Fig. 3. The centroids of putative old-forest species in the NMS ordination space of polypore assemblages on 2-ha plots in Estonian forests (**II**). The polygons delineate assemblages in different forest types and management stages (**A** – all forests and harvested plots; **B** – subset of mature managed and old-growth plots in three mixedwood types). The x- and y-axes explain 48% and 26% of the variation in **A**; and 40% and 21% in **B**, respectively. The species with significant indicator value for old growth are shown in **boldface**.
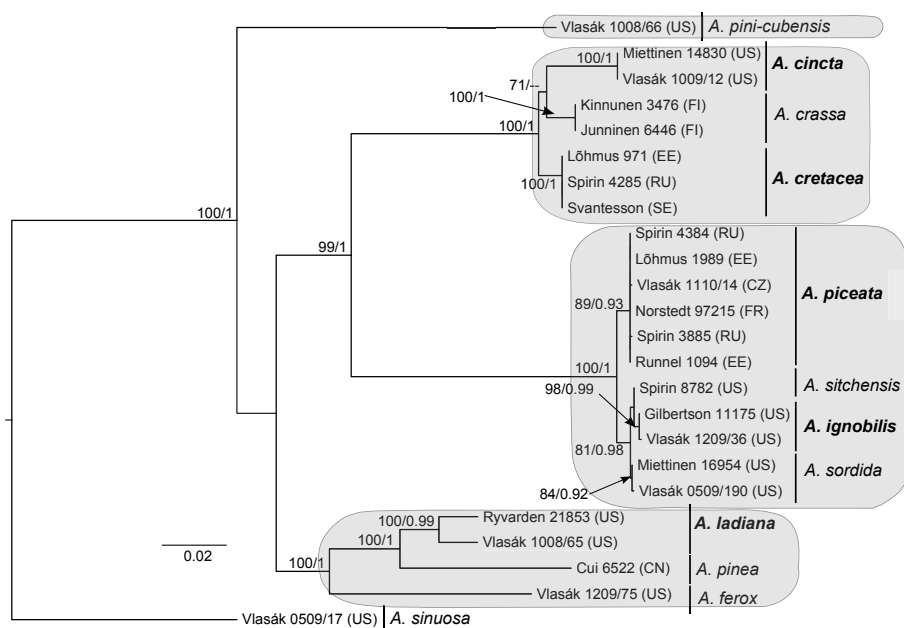
Fig. 4. Phylogenetic relationships of species in the *Antrodia crassa* group, inferred from Maximum-Likelihood analysis of combined three-gene (ITS-LSU-*tef1*) dataset (**IV**). Maximum-Likelihood branch bootstrap (>70) and posterior probability scores (>0.85) are given. The scale bar indicates substitutions per nucleotide position. Four main clades of species related to *A. crassa* are shaded.

3.3 Managed forests as fungal habitats (II; V–VI)

For polypores, the habitat value of managed forests was mainly determined by substrate amount and diversity, and that effect was also forest type dependent (**II**). Total species pools differed only little between the old-growth (117 species in 23 plots) and mature managed forests (110 species in 23 plots); additionally, 46 harvested plots hosted 109 species. However, stand-scale assemblage composition differed between all management stages, including old-growth–mature managed forest contrasts in all forest types. In the three mixedwood types (meso-eutrophic; eutrophic; swamp), CWD amount was the main factor for assemblage differentiation of mature and old-growth stands; most distinctly in eutrophic forests (**II**: Fig. 5B). In mixedwood (but not in the pine-dominated *Vaccinium*-type), old growth was also clearly more species-rich (Fig. 5A). The species-richness had a threshold response to general substrate availability (CWD volume) when analyzed across all studied forest management stages: up to ca. 60 m^3/ha, CWD additions abruptly increased the mean number of species, but the effect varied a lot (Fig. 5B). In mature and old forests, the variation in species-richness was best explained by forest type, volume of downed spruce

CWD, and CWD species diversity (**II**: Table 1). The latter effects were linear and the model outperformed the threshold model depicted on Fig. 5B.

Important characteristics of dead retention trees in post-harvest sites differed for polypores and lichens, but tree species and dead-wood type mattered most for both (**V**: Table 3). Pooled tree-scale species-richness was highest on those trees that had died by trunk breakage creating both a snag and a log. Polypores were most species-rich on large fallen aspens; the aspens that had died 8–10 years ago hosted 11 species of conservation concern. The most species-rich assemblages of epixylic lichenized and allied fungi inhabited pine snags; the diversity increased also with wood exposure and time since tree death (colonisation time). Snags of pre-harvest (forest) origin were most distinct in birch: only six such snags hosted twice as many epixylic lichens than all the 33 birch snags created from retention trees together (**V**). The minimum sets of retention trees for representing fungal diversity depended on the conservation target. The set for representing just common species comprised only 15 trees, with roughly equal proportions of tree species (40% aspen, 27% birch, 33% pine); an almost three times larger set (41 trees: 39% aspens, 24% birches, 37% pines) was needed to represent all sampled species. Targeting species of conservation concern resulted in the least balanced set with 50% aspens (preferably the largest), 40% pines (preferably trunk-broken) and 10% birches (preferably fallen) among the 20 trees.
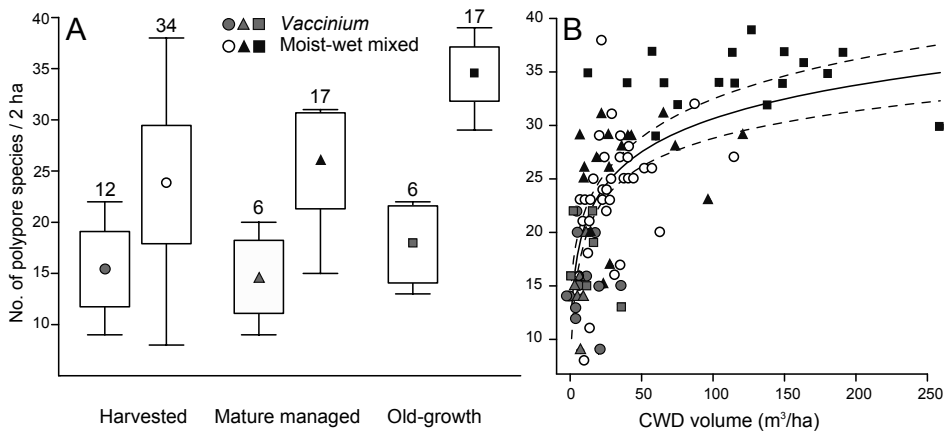

Fig. 5. Polypore species-richness in 2-ha plots (n = 92; four-hour surveys) by management stage and *Vaccinium*- vs. other forest types. (A) summarizes arithmetic means (points), standard deviations (boxes), the range (whiskers) and sample sizes (numbers). (B) shows a logarithmic relationship with the amount of downed CWD ($R^2 = 0.48$; ± 95% CI). (**II**)

Case-study **VI** provided evidence that tree species diversity alleviates local extinction risks for associated fungi. In a forest affected by ash dieback, about half of ash trees were killed in five years and the proportion of healthy trees

dropped dramatically. Large ash trees were the main habitat for several remnant populations of lichenized fungal species, including five populations of national conservation concern. The dieback extirpated one of those species (*Pyrenula laevigata*) and three more (*Chaenotheca phaeocephala, Cetrelia olivetorum, Arthopyrenia cinereopruinosa*) became endangered, with populations on dead or dying trees only. The most abundant species of conservation concern, *Lobaria pulmonaria* (ca. 730 thalli on 74 trees), had 92% of its total population on ash trees in 2008 and two-thirds of the large colonies surviving until 2012 occupied dying or recently dead trees (Fig. 6). However, the presence of alternative hosts (notably *Ulmus* and *Acer* in the subcanopy) enabled *L. pulmonaria* to colonize at least five new trees and seven new thalli emerged on previously occupied trees. The occupied *Ulmus* trees were larger than the rest of cohort and they had more 'source trees' within 30 m (Fig. 6).
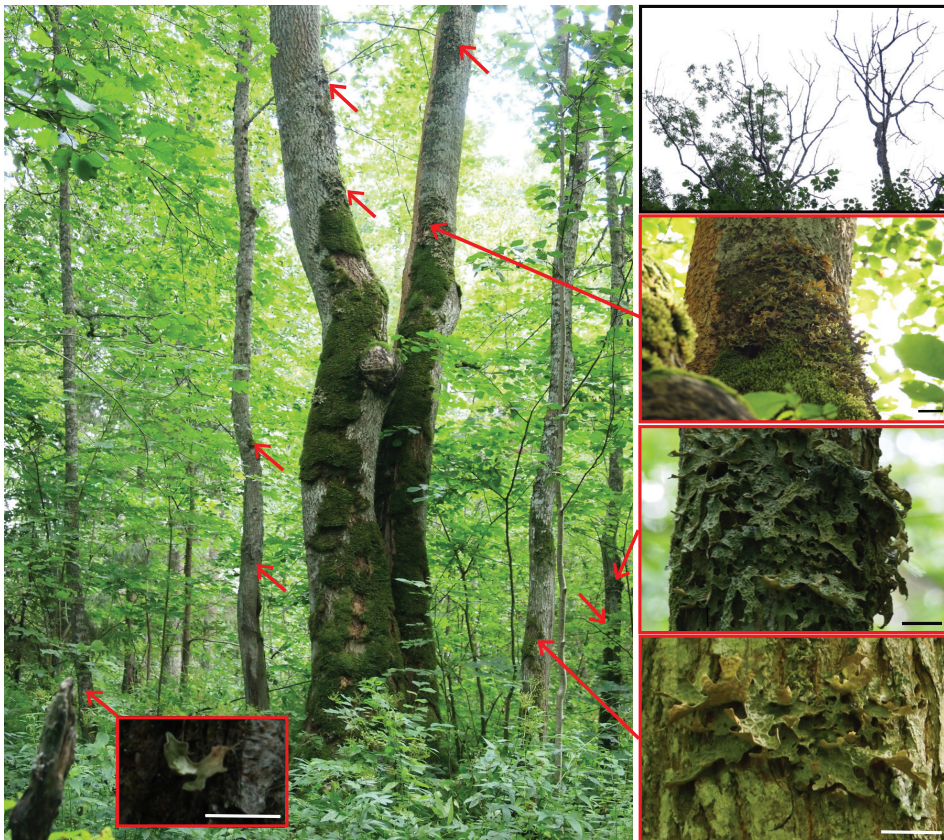

Fig. 6. Overstorey ash trees with large colonies of *L. pulmonaria* ('source trees') support its establishment on the surrounding subcanopy *Ulmus* and *Acer* trees. Upper right: canopy views of the ash trees (the tree on the left retains 5% crown). The arrows indicate thalli of *L. pulmonaria*, with a subset depicted on the small photos (Right: a typical large patch on the source tree and the two largest on *Ulmus*. Left: small thallus on a recently colonized *Ulmus*. Scale bar = 1 cm). (**VI**)

4. DISCUSSION

4.1 Fungal surveys: combining fruit-body and molecular sampling

The potential bias of fruit-body surveys is to date a central problem in most ecological studies that describe assemblages of non-lichenized fungal species. The main result in the methodological study **I** was that the fruit-bodies of most polypore species can be found in close vicinity of their molecular detections, even if they are absent on the sampled tree. Hence, given sufficient plot size, the "fruiting bias" is unlikely to undermine the results of ecological surveys based on fruit bodies. Sufficient plot size may depend on the study aim, the fungal group, and distribution of specific substrates (see also Hunter & Webb 2002). At least the assemblage surveys on 2-ha plots (papers **I–III**) appeared both effective and cost-efficient for assessing the diversity of polypores in Estonia. In the case of small study plots (<0.3 ha as suggested by study **I**) or in tree-scale surveys, the fruiting-bias is probably more pronounced. In such cases combining fruit-body surveys with molecular sampling, or repeated inventories (as in study **V**) might be necessary for obtaining reliable results (see also Abrego et al. 2016).

Nevertheless, there are at least two good reasons to supplement fungal fruit-body surveys with molecular identification of mycelia. First, molecular methods enable snapshots of broad fungal diversity even in the case of limited samples, including fungi that do not produce fruit-bodies at all or only do so ephemerally (e.g., Porter et al. 2008; Rajala et al. 2012). Secondly, as illustrated by study **II,** including non-fruiting mycelia in habitat assessments of threatened species may widen the understanding of their habitat associations. More specifically, the modelling of fruit-body distribution of the old-forest polypore *Fomitopsis rosea* suggested that this species may inhabit finer spruce fractions in production forests without producing fruit-bodies. These habitats may be vital for maintaining population connectivity (possibly through mycelial dispersal by beetles; see Johansson et al. 2006).

4.2 Old-forest associated fungi

The study **II** (complemented with studies **III–IV**) showed that old-forest associations of polypores are diverse and context dependent; they require critical treatment for effective species protection and listing of indicators for practical use. Most studies on such associations have to date been performed in a limited geographic area (mostly Fennoscandia) and in a specific ecological context (mostly landscapes with extreme contrasts between protected and managed forests) (Lonsdale et al. 2008). It is largely unknown how these studies translate to other settings. Also, species delimitation has undergone huge

changes within most fungal groups in the past decades (e.g., Lumbsch & Leavitt 2011; Kõljalg et al. 2013). The species lists used for habitat protection would be particularly important to update because most such lists are based on past expert opinions that represent a variable input of balanced scientific data.

Study **II** showed that, in Estonia, the old-forest associations of polypores are relatively weak: only a subset of old-forest species documented in Fennoscandia was confined to old-growth. Most of such species are considered over-average demanding towards habitat connectivity and/or availability (e.g., Penttilä et al. 2006; Nordén et al. 2013). However, study **II** did not assess some of the most sensitive polypores, e.g., *Amylocystis lapponica* and *Pycnoporellus alboluteus*, which are already extremely rare in Estonia. The latter species certainly warrant protection of their old-forest habitat, but they are not frequent enough for regional use as indicators (cf. Caro 2010). Interestingly, both *A. lapponica*, *P. alboluteus* and several other extreme rarities and regionally extinct taxa (Parmasto 2004) as well as half of the species on our short list of Estonian old-forest polypores are all spruce-dwelling. In contrast, the putative old-forest species living on deciduous trees showed generally low dead-wood requirements and most of them were abundant also in managed forests (**II**). The only clearly old-forest associated deciduous-dwelling polypore – *Rigidoporus corticola* on aspen – can, in fact, also live in fallen retention trees in aspen-rich managed landscapes (Junninen et al. 2007; study **V**). Such differences in old-forest associations between ecological groups confirm that the strength and nature of these associations depend on regional forest conditions and management history.

In Estonia, stand-scale substrate abundance was clearly the dominant factor in shaping old-forest associations of polypores (**II**). These results are in accordance with the habitat associations of calicioid ascomycetes (pin lichens) – another group of fungi inhabiting dead wood and old living trees – studied in the same system (Lõhmus & Lõhmus 2011). In more constrasting forest landscapes, the old-forest affinity of both polypores and calicioid fungi has been attributed to their sensitivity to forest fragmentation, i.e., to dispersal limitation instead (Tibell 1992; Penttilä et al. 2006; Berglund & Jonsson 2008; Stokland & Larsson 2011). Because fragmentation effects were only weakly supported by study **II**, one can hypothesise that old-forest associated polypores (particularly those inhabiting spruce) represent different ecological strategies. (i) The typical fragmentation-sensitive species that are strong competitors but moderate dispersers (e.g., Holmer & Stenlid 1997). In Estonia, only a subset of such species appears old-forest associated; they include some polypores inhabiting specific substrates, notably large spruce trunks. (ii) The species that require high substrate amounts, which most typically develop after disturbance in fluctuating, possibly semi-open conditions. On managed landscapes, the distribution of such disturbance-favouring species probably follows that of CWD hotspots, including old-growth remnants, large windthrows (e.g., following the outbreaks of root-rot fungi), and occasional clear-cuts.

The studies **III** and **IV** on *Antrodia* species illustrate how the performance of fungal indicator species lists may be hampered by unresolved taxonomy. Cryptic species are common among fungi (Hawksworth 2001), and the examples presented in my thesis add to other cases where "well-known old-forest species" appear to represent several ecologically distinct lineages (e.g., Kauserud et al. 2007; Spirin et al. 2015). Also, *Cinereomyces vulgaris* – one of the few old-forest associated polypores in study **II** – was in our molecular data represented by two closely related but distinct lineages (K. Runnel, unpublished analyses). An unfortunate consequence of unrecognized cryptic species is that their specific habitats or functions may be overlooked in ecological studies and conservation. Such bias could be significantly reduced by focused molecular analyses of atypical fungal samples; study **III** proposed a standard procedure for that. On a more general level, the studies **II** and **III** exemplified the necessity for, and benefits of, a wider cooperation between taxonomists and ecologists. While ecological sampling designs can promote new and interesting taxonomical hypotheses, ecologists would obviously benefit from reduced 'taxonomical noise' in their species-level datasets. Such cooperation could eventually also lead to taxonomically and ecologically up-to-date indicators for practical use, which could improve the current level of guidance provided by mycologists to forest conservation and management issues (Molina et al. 2011).

A general conclusion from studies **II** and **III** is that conservation practices might benefit from fewer, but better supported fungal indicators. The so-far proposed lists of old-forest fungi remain nevertheless useful as sources of working hypotheses for taxonomic and ecological work. However, in practical conservation, they might be replaced with a process-based set of focal species (sensu Lambeck 1997; 2002), which form well-established taxonomic entities and have been confirmed to be sensitive to a particular habitat change in replicated studies. When fungal species-level arguments are needed for selecting protected areas, it may be more justified and straightforward to use regional red lists rather than the proposed indicators.

4.3 Managed forests as fungal habitats

My thesis demonstrates that fungi inhabiting dead wood and old living trees (including putative old-forest specialists) may form species-rich assemblages also in managed forests (see also Lõhmus & Lõhmus 2011). This is possible if these forests are diverse in terms of tree species, dead-wood structures, and successional stages, including old stands. These important forest characteristics are, however, under a high pressure of forestry traditions and economic expectations (e.g., Puettmann et al. 2009). Even in the most democratic societies, where sustainable forest management has become politically well established, spontaneous trends in forestry tend to deviate from sustaining full biodiversity (Lindahl et al. 2016). Getting the facts right is one assumption for a successful combination of conservation and forest management aims.

The importance of tree species diversity was revealed from three different angles in this thesis. Study **II** suggested that tree species diversity is a major cause for the threshold relationship between CWD availability and polypore species-richness (e.g., Junninen & Komonen 2011): at least in the North-European conditions, each added tree species tends to contribute with its specific fungi. Study **V** explored polypore and epixylic lichen diversity on dead retention trees. It found that an intuitive and simple management guideline for tree retention at harvest – to retain all tree species in equal amounts – may well be justified because of the complementary habitat qualities of tree species. However, more selective decisions can be made once the actual threatened taxa in a region are distinguished. Study **VI** complemented these findings with the observation that tree species diversity may additionally buffer the effects of severe natural disturbance in forests. When a pathogen causes massive dieback of one tree species (here: *Fraxinus excelsior*), rare epiphytes using these trees may escape local extirpation if alternative host tree species are available (here: *Ulmus* and *Acer*). Interestingly, these particular tree species host relatively few specialist polypores (Niemelä 2008), which probably explains why study **II** did not detect reduced polypore diversity along with the scarcity of the hard-wooded deciduous trees in Estonian managed forests (Lõhmus & Kraut 2010). Hence, different sets of trees are important for different fungal groups.

Studies **II–VI** showed that, in the presence of necessary substrates (large living trees, standing and downed dead wood), several putative old-forest species can inhabit managed forests, including harvested sites. Some rare species requiring high substrate amounts (e.g., *Antrodia cretacea*; **III–IV**; see also Chapter 4.2) can specifically favour high amounts of downed dead wood after the harvest. Green tree retention can further improve such habitat by providing a decades-long supply of large dying trees for some early-successional fungi that might otherwise disappear from the landscape (such as *Funalia trogii*; **V**). Other species can benefit from specific dead-wood substrates (e.g., *Diplomitoporus flavescens* on pine snags) or from habitats with improved connectivity (e.g., *Rigidoporus corticola*). All these main functions correspond to the original theoretical considerations behind the retention approach (Franklin et al. 1997).

Retaining dead wood and old living trees for maintaining biodiversity in managed forests requires special planning. In terms of fungal conservation, the strongest conflict in rotational forestry is the reduction of slowly developing woody structures: old live trees are harvested (cf. **VI**) and fellings destroy most snags (Lõhmus et al. 2013) that host specific slowly developing epixylic assemblages (**V;** Lõhmus & Lõhmus 2001). Since live spruce trees are seldom retained for their vulnerability to windfall (Rosenvald et al. 2008; Rosenvald & Lõhmus 2008), large downed spruce trunks (crucial for several old-forest associated polypores; **II**) rarely develop in managed forests. In addition to improving tree retention practices, dead-wood habitats could be diversified by controlled burning, as burned substrates may be colonized by several specific and rare fungal species (Suominen et al. 2015).

The species-richness and occurrence of specific fungi in the studied mature managed forests (**II**, **VI**) obviously depended on the actual age range of these forests, which is limited by rotation age. While the biodiversity consequences of the prevalent trends towards lowering the forest rotation age may be unclear in details, an overall negative effect is well established (Roberge et al. 2016). For example, the forest site in study **VI** hosted a particularly rich lichen assemblage (Lõhmus et al. 2012), although it was just slightly older than the normal felling age. Instead of clear-felling, the forest had experienced some partial harvest, which was only slightly different from the current tradition (Lõhmus et al. 2012, see also Jüriado & Liira 2009). Thus, instead of lowering rotation ages throughout managed forests, a better compromise might be to diversify these between stands. The general conclusion from studies **II**, **V** and **VI** is, therefore, that there are many possibilities for adjusting forest management to better address the fungal diversity on dead wood and old living trees.

KOKKUVÕTE

Seentest lähtuvad argumendid metsade looduskaitses

Seened on liigirikas ning funktsionaalselt mitmekesine organismirühm, kelle üheks olulisemaks elupaigaks on metsad. Valdav osa metsi on tänapäeval inimmõjulised, kuid seda, kuidas inimtegevus on mõjutanud seenestikku ja sedakaudu metsaökosüsteemide toimimist, tuntakse üllatavalt halvasti. Üks osa niisugusest inimmõjust on metsamaastiku struktuuriline vaesumine, st spetsiifiliste elupaikade nappus.

Paljude metsaseente elutsükkel on seotud kõdupuiduga, kus domineerivad saprotroofid, ja põlispuudega, mille maapealseid osi asustavad epifüütsed samblikud ja parasiitseened. Tüüpilistes majandusmetsades on selliste „jäänukstruktuuride" hulk ja mitmekesisus märkimisväärselt vähenenud. Teatud puuliigid ning stabiilset elupaika pakkuvad jämedad lamatüved ja tüügaspuud võivad majandusmetsas peaaegu täielikult puududa, elusatel puudel aga ei jõua tavapärase raieringi jooksul tekkida mitmed seentele olulised mikroelupaigad (näiteks vanade puude rõmeline korp). Kuna jäänukstruktuure napib, võib nende asustamine majandusmetsas hakata sõltuma liikide levimisvõimest ning fragmenteerunud metsamaastikus võivad samaväärsed elupaigad olla loodusmetsaga võrreldes liigivaesemad.

Siinne doktoritöö keskenduski kõdupuitu ja põlispuid asustavatele seentele, eriti torikseentele (morfoloogiline rühm puitu lagundavaid kandseeni). Kahes uuringus käsitleti ka samblikke (lihheniseerunud kottseeni), kes asustavad paljandunud puidupindasid (epiksüülsed samblikud) või suurte vanade puude korpa. Paljusid nende liigirühmade liike leitakse tänapäeval enamasti põlismetsafragmentidest, kuid põlismetsaseose ökoloogilised põhjused ei ole enamasti täpselt teada. Looduskaitseliselt on oluline eristada, kas liik ei suuda majandusmetsas elada sobilike elupaikade puudumise või levimispiirangute tõttu. Ehkki mõnda halva levimisvõimega liiki võibki olla võimalik säilitada ainult kaitsealadel, võiks teiste liikide soodsa seisundi tagamine olla võimalik ka keskkonnasõbralikumate metsandusvõtete toel. See võiks toetada ka ökoloogiliste funktsioonide mitmekesisust majandusmetsades.

Peale selle, et paljud kõdupuitu ja põlispuid asustavad seened on ise ohustatud ja kaitse all, kasutatakse neid looduskaitses ka indikaatoritena teiste metsaväärtuste tuvastamisel. Üks tuntumaid näiteid on hästimärgatavate indikaatorliikide kasutamine haruldaste liikide koondumiskohtade (vääriselupaikade) määratlemiseks majandataval metsamaastikul. Praktikutele mõeldud indikaatorliikide nimekirjad on aga enamasti koostatud ilma eelnevate uuringuteta (ekspertarvamuste põhjal) või üle võetud teistest piirkondadest. Peaaegu uurimata on seente kasutusvõimalused säästva metsanduse suunisliikidena, st liikidena, mis võimaldaksid kuluefektiivselt jälgida ja kujundada ökosüsteemide terviklikkust. Seened võiksid indikeerida näiteks olulisi ja varjatud kõdunemisprotsesse (näiteks tüvemädanikke, mis kujundavad puuõõnsusi) ning metsamaastiku elupaigalist sidusust.

Doktoritöö põhieesmärgiks oli hinnata erinevate kasutatavate metsakaitse ja -majandusmeetodite olulisust seeneliikide kaitsel. Töö oluliseks osaks oli seente põlismetsaseoste kriitiline käsitlus oludes, kus poollooduslik metsandustraditsioon võimaldab paljude seentele oluliste substraatide teket ja püsimist ka majandusmetsades. See võimaldab eristada põlismetsade hävimise mõju intensiivsete metsakasvatusvõtete omast majandusmetsades.

Torikseente uurimisel olid töö põhimeetodiks viljakehadel põhinevad liigiinventuurid puistu mastaabis, mille adekvaatsust kontrolliti uuringus **I**. Nimelt ei pruugi puutüves mütseelina elavad torikseened olla inventuuril leitavad, sest viljakehade moodustamine sõltub paljudest asjaoludest ja on raskesti ennustatav. Molekulaarselt (uue põlvkonna sekveneerimine Illumina platvormil) puidust määratud seenekooslusi uurides leiti, et ehkki ühe puutüve piires jääb liik viljakehana tõenäoliselt tõesti tuvastamata, on suur tõenäolisus leida sama liigi viljakeha mõnelt teiselt puutüvelt lähikonnas (75% juhtudest 30 m raadiuses). Viljakehapõhiste inventuurimeetodite täiendamine molekulaarsetega on siiski oluline, sest viimased võimaldavad kiirülevaadet kõigist seenerühmadest ning lisaks aitavad hinnata ohustatud liikide levikut mütseelina.

Uuringud **II** ja **III** võrdlesid torikseente levikumustreid põlismetsades, küpsetes majandusmetsades ja raiesmikel. Uuring **II** näitas, kuidas liikide elupaigaseosed sõltuvad piirkondlikust metsandustavast. Seni on torikseeni kõige rohkem uuritud Fennoskandias, kus majandusmetsad on ulatuslikult vaesunud ja paljud liigid sõltuvad allesolevate põlismetsade kaitsest. Eestis, kus metsamaastik on struktuuriliselt mitmekesisem, tuvastati põlismetsaseos ainult kümnel liigil, kusjuures ka nende liikide koondumine põlismetsa oli põhiliselt tingitud spetsiifilisest substraadivajadusest (nt suured lamakuused). Ainult kahte liiki mõjutas ka metsa elupaigaline sidusus: *Fomitopsis rosea* (roosa pess) ja *Rigidoporus corticola* (haavatarjak). Uuring **III** ja selle taksonoomiline edasiarendus **IV** demonstreerisid, et liigi elupaigaseoseid ja indikaatorväärtust ei saa määratleda ilma adekvaatse valimivõtu ja tänapäevase molekulaartaksonoomilise käsitluseta. Selgus, et Põhjamaades tuntud põlismännikute indikaatorliigi *Antrodia crassa* (paks korgik) asemel asustab Eestis (ja Kesk-Euroopas) kuuski selle välimuselt sarnane sõsarliik *A. cretacea* sp. nova. Viimane on häiringuliik, kes elab ka avakooslustes, kus leidub ohtralt sobivat lamapuitu. Praktilised järeldused nendest uuringutest on, et küsitavate „indikaatorliikide" asemel tuleks kaitsealade planeerimisel lähtuda pigem otseselt ohustatud liikidest. Majandusmetsade elupaigakvaliteedi kohta võiksid aga infot anda vähesed hästi uuritud suunisliigid, mille tundlikkus kindlate elupaigaomaduste suhtes on teadusuuringutes kinnitust leidnud (nt ülalnimetatud *Fomitopsis rosea* ja *Rigidoporus corticola*).

Doktoritöö näitas, et enamik kõdupuitu ja põlispuid asustavaid seeneliike (sh mitmed põlismetsaseoseliseks peetud liigid) saavad elada ka majandusmetsades, kui seal leidub erinevaid puuliike ning piisavalt jäänukstruktuure. (i) Puude liigiline mitmekesisus osutus üheks põhiliseks torikseente liigirikkust selgitavaks faktoriks (**II**). Seetõttu tuleks nii torikseente kui puidusamblike jaoks tavajuhtudel jätta raiesmikele säilikpuudeks võrdselt erinevaid puuliike (**V**).

Uuring **VI** näitas, et pikas perspektiivis stabiliseerib puistu puuliigiline mitme-kesisus ka looduslike häiringute mõju seenekooslustele. Uuriti liigi *Lobaria pulmonaria* (harilik kopsusamblik) populatsiooni, mis asustas põhiliselt suuri vanu saarepuid – neist enamik suri aga saaresurma tõttu mõne aasta jooksul. See samblikupopulatsioon säilis tänu kohapeal leidunud niisugustele alternatiiv-setele peremeespuudele, mis majandusmetsas enamasti enne sobivaks kujune-mist raiutakse (vanad haavad ning teise rinde jalakad ja vahtrad). (ii) Jäänuk-struktuuride puhul on olulised nii nende hulk kui ka mitmekesisus. Näiteks looduslikult uuenevad säilikraiesmikud pakuvad rohke lamapuidu korral elupaika haruldastele häiringuliikidele ning surnud säilikmänni-tüügastest kujuneb vajalik substraat epiksüülsetele samblikele (**II–V**). (iii) Kõige raskem on majandatud metsades tagada aeglase tekkega jäänukstruktuuride esindatust. Näiteks hävib lõppraiel enamik epiksüülsete samblike elupaikadest (loodusliku tekkega tüügaspuud; **V**) ja tavapärane lõppraievanus ei soosi torikseentele olulise elupaiga, jämedate lamakuuskede teket (**II**). Mõned ohustatud liigid saavad aga hästi hakkama metsanduslikus mõttes „üleseisnud" metsas, mida majandatakse väheintensiivsete valikraietega (**VI**). Seetõttu tasuks kaaluda puistute raievanuste diferentseerimist majandusmetsades.

Kokkuvõttes leidub metsamajanduse ning põlispuid ja kõdupuitu asustavate seente elurikkuse edukaks kombineerimiseks mitmeid võimalusi, kuid see eeldab poliitilist tahet ning säästva metsanduse teaduspõhist planeerimist.

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PUBLICATIONS

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Scientific publications:

Runnel, K., Ryvarden, L. 2016. *Polyporus minutosquamosus* sp. nov. from tropical rainforests in French Guiana with a key to neotropical species of Polyporus (Polyporaceae, Basidiomycota). Nova Hedwigia, xx, xx−xx [in press].

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Conference presentations:

Fungi of Central European Old-Growth Forests, 14.–17.09.2015, Český Krumlov, Czech Republic; oral presentation

Forest landscape mosaics: disturbance, restoration and management at times of global change, 11.–14.08.2014, Tartu, Estonia; oral presentation

3rd European Congress of Conservation Biology, 28.08–2.09.2012, Glasgow, United Kingdom; oral presentation

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Teaduspublikatsioonid:

Runnel, K., Ryvarden, L. 2016. *Polyporus minutosquamosus* sp. nov. from tropical rainforests in French Guiana with a key to neotropical species of Polyporus (Polyporaceae, Basidiomycota). Nova Hedwigia, xx, xx−xx [ilmumas].

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