JYU DISSERTATIONS 42

Jenna Purhonen

Dead Wood and Fungi: Detection, Diversity and Conservation in Boreal Forests

UNIVERSITY OF JYVÄSKYLÄ
FACULTY OF MATHEMATICS
AND SCIENCE

JYU DISSERTATIONS 42

Jenna Purhonen

Dead Wood and Fungi: Detection, Diversity and Conservation in Boreal Forests

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA303
joulukuun 14. päivänä 2018 kello 12.

Academic dissertation to be publicly discussed, by permission of
the Faculty of Mathematics and Science of the University of Jyväskylä,
in building Ambiotica, hall YAA303, on December 14, 2018 at 12 o'clock noon.

JYVÄSKYLÄN YLIOPISTO
UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2018

Editors
Jari Haimi
Department of Biological and Environmental Science, University of Jyväskylä
Ville Korkiakangas
Open Science Centre, University of Jyväskylä

Cover photo by Panu Halme.

Permanent link to this publication: http://urn.fi/URN:ISBN:978-951-39-7620-0

ISBN 978-951-39-7620-0 (PDF)
URN:ISBN:978-951-39-7620-0
ISSN 2489-9003

ABSTRACT

Purhonen, Jenna
Dead wood and fungi: detection, diversity and conservation in boreal forests
Jyväskylä: University of Jyväskylä, 2018, 49 p.
(JYU Dissertations
ISSN 2489-9003; 42)
ISBN 978-951-39-7620-0 (PDF)
Yhteenveto: Lahopuu ja sienet: havaitseminen, monimuotoisuus ja suojelu boreaalisissa metsissä
Diss.

Dead wood and associated fungal communities are a crucial part of boreal forest ecosystems, and severely affected and threatened by human actions like commercial timber harvesting. Despite their importance for forest functioning, most wood-inhabiting fungal species, especially those producing small fruit bodies, are still ecologically and taxonomically poorly known. In addition, studies on dead wood profiles have neglected fine woody debris. This thesis includes detailed investigations of fruiting phenology of different morphological groups and complete dead wood profile of one semi-natural boreal forest. In addition, the diversity patterns of wood-inhabiting fungal communities according forest continuity and naturalness as well as dead wood quality were studied in 14 semi-natural forests. In addition to species richness the relationship between species traits and substrate quality was explored. The fruiting phenologies and dead wood profiles differed between fungal groups and dead wood tree species, respectively. Forest continuity and naturalness had a positive but weak effect on species richness, substrate continuity being important for *Micarea* lichens. Tree species had strong influence on fungal community composition. Broadleaved dead wood hosted the highest species richness, especially discomycetoid and pyrenomycetoid fungi specializing on it. Pileate fungi were found specializing on spruce and were the only group having positive response to forest naturalness at the substrate level. Especially discomycetoid and pyrenomycetoid fungi inhabiting pine had positive relationship with forest naturalness at the site level. Species had on the average larger spores on broadleaved than conifer dead wood, and the spore size increased with log size. In conserving dead wood and its fungal inhabitants, the tree species- and fungal group-specific responses need to be taken into account. Standing and downed dead pine is a special case as considering species inhabiting it in management planning requires time scale of a millennium rather than centuries.

Keywords: Community; forest management; fruit body; habitat quality; species richness; spore; functional trait.

Jenna Purhonen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author's address Jenna Purhonen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
jenna.purhonen@jyu.fi

Supervisors Docent Panu Halme
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Docent Atte Komonen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Docent Seppo Huhtinen
Herbarium, Biodiversity Unit, University of Turku
FI-20014 Turku
Finland

Reviewers Professor Anne Sverdrup-Thygeson
Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences
Høgskoleveien 12, N-1433 Ås
Norway

Docent Olli-Pekka Tikkanen
School of Forest Sciences
University of Eastern Finland
P.O. Box 111
FI-80101 Joensuu
Finland

Opponent Associate Professor Mari T. Jönsson
ArtDatabanken
P.O. Box 7007
75007 Uppsala
Sweden

TIIVISTELMÄ

Purhonen, Jenna
Lahopuu ja sienet: havaitseminen, monimuotoisuus ja suojelu boreaalisissa metsissä
Jyväskylä: University of Jyväskylä, 2018, 49 p.
(JYU Dissertations
ISSN 2489-9003; 42)
ISBN 978-951-39-7620-0 (PDF)
Yhteenveto: Lahopuu ja sienet: havaitseminen, monimuotoisuus ja suojelu boreaalisissa metsissä
Diss.

Lahopuu ja sen sieniyhteisöt ovat olennainen osa boreaalisten metsien ekosysteemiä ja jatkuvasti ihmisen vaikutuksen alaisina muun muassa metsienkäsittelyn takia. Vaikka lahopuiden sienet ovat elintärkeitä metsien toiminnalle, useimmat niistä ovat ekologisesti ja taksonomisesti huonosti tunnettuja. Lisäksi metsien lahopuuprofiilitutkimuksissa ei ole otettu juuri pienikokoista lahopuuta huomioon. Tämä väitöskirja sisältää yksityiskohtaisen selvityksen erilaisten lahopuun sieniryhmien itiöemien muodostamisen fenologiasta yhdessä luonnontilaisen kaltaisessa boreaalisessa metsässä ja tämän metsän lahopuuprofiilista. Lahopuun sieniyhteisöjen monimuotoisuutta selvitettiin suhteessa metsän jatkuvuuteen, luonnontilaisuuteen ja lahopuiden laatuun 14:ssa luonnontilaisen kaltaisessa metsässä. Lajirikkauden lisäksi tutkittiin lajien ominaisuuksien ja lahopuun laadun välisiä yhteyksiä. Eri sieniryhmien itiöemäfenologiat ja puulajien lahopuuprofiilit erosivat toisistaan. Metsän jatkuvuudella ja luonnontilaisuudella oli positiivinen, mutta heikko yhteys sienten lajirikkauteen, rungon jatkuvuuden ollessa tärkeä *Micarea*-jäkälille. Puulajilla oli voimakas vaikutus sieniyhteisöjen koostumukseen. Lehtipuilla oli korkeampi lajirikkaus kuin havupuilla, ja erityisesti maljamaiset ja pullomaiset lajit olivat erikoistuneet sille. Lakilliset sienet olivat erikoistuneet kuusen lahopuulle, ja ne olivat ainoa ryhmä, jonka lajirikkaudella oli positiivinen yhteys metsän luonnontilaisuuteen runkotasolla. Kohdetasolla männyn maljamaisten ja pullomaisten ryhmien vaste luonnontilaisuuteen oli positiivinen. Lehtipuulla esiintyvillä lajeilla oli keskimäärin suuremmat itiöt, kun havupuulla, ja itiökoko kasvoi myös rungon koon kasvaessa. Väitöskirjani tulokset osoittavat, että lahopuun ja sen sienilajien suojelussa puulaji- ja sieniryhmäkohtaiset vasteet on otettava huomioon. Pystyyn kuolleet ja maapuumännyt ovat erityistapaus, sillä niiden lajiston huomioonottaminen metsienkäsittelyn suunnittelussa vaatii aikajaksoja, jotka ovat ennemmin vuosituhansien kuin vuosisatojen mittaisia.

Avainsanat: Elinympäristön laatu; itiö; itiöemä; lajirikkaus; metsänkäsittely; toiminnallinen ominaisuus; yhteisö.

Jenna Purhonen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I–V.

I Purhonen J., Huhtinen S., Kotiranta H., Kotiaho J. S. & Halme P. 2016. Detailed information on fruiting phenology provides new insights on wood-inhabiting fungal detection. *Fungal Ecology* 27: 175-177.

II Halme P., Purhonen J., Marjakangas E., Komonen A., Juutilainen K. & Abrego N. 2018. Dead wood profile of a semi-natural boreal forest - implications for sampling. Submitted manuscript.

III Saine S., Aakala T., Purhonen J., Launis A., Tuovila H., Kosonen T. & Halme P. 2018. Effects of local forest continuity on the diversity of fungi on standing dead pines. *Forest Ecology and Management* 409: 757–765.

IV Purhonen J., Abrego N., Komonen A., Huhtinen S., Kotiranta H., Læssøe T. & Halme P. 2018. Varying effects of forest naturalness on different morpho-groups of wood-inhabiting fungi. Manuscript.

V Purhonen J., Ovaskainen O., Halme P., Komonen A., Huhtinen S., Kotiranta H., Læssøe T. & Abrego N. 2018. Morphological traits predict host-tree specialization in wood-inhabiting fungal communities. Manuscript.

The table shows contribution of authors in different stages of the research included into this thesis. The order of the authors indicates the relative proportion of contribution, the first author having the largest and the last the smallest share.

	I	II	III	IV	V
Planning	PH, JP	PH, JP, KJ	SS, PH, TA	PH, JP	JP, NA
Data	JP, PH, SH, HK	PH, KJ, EM	SS, TA, HT, AL, PH, JP, TK	JP, NA, PH, SH, HK, TL	JP, NA, PH, SH, HK, TL
Analyses	JP	PH, JP	SS, TA	JP	NA, OO, JP
Writing	JP, PH, JK, HK, SH	PH, JP, AK, EM, NA, KJ	SS, JP, PH, TA, TK, HT, AL	JP, AK, PH, NA, HK, SH, TL	JP, NA, OO, AK, PH, HK, SH, TL

JP = Jenna Purhonen, PH = Panu Halme, NA = Nerea Abrego, AK = Atte Komonen, SS= Sonja Saine, TA = Tuomas Aakala, KJ = Katja Juutilainen, TK= Timo Kosonen, JK = Janne S. Kotiaho, SH = Seppo Huhtinen, HK = Heikki Kotiranta, OO = Otso Ovaskainen, TL = Thomas Læssøe, EM = Emma-Liina Marjakangas, HT = Hanna Tuovila, AL = Annina Launis

1 INTRODUCTION

1.1 Looking at the big picture

The inspiration for this thesis comes from an intrinsic place - a genuine interest to explore the unknown. Diving into the fascinating world of poorly known wood-inhabiting fungi is analogous to the early explorers discovering islands never visited by human before, asking questions like, how many and what kind of species there are, and most importantly, why these species are there?

Actually, from the point of view of wood-inhabiting fungi a dead wood piece is an island situated on a larger island - the forest. Both are surrounded by a hostile sea of non-habitat. The exception is that these islands are dynamic in much shorter time scales than the actual oceanic islands. This specific nature of the habitat of wood-inhabiting fungal communities makes it interesting to study different questions at different spatial and temporal scales ranging from microhabitats to landscape level and over time.

The motivation comes also from the lack of knowledge considering the conservation needs of poorly known fungal species inhabiting different kinds of dead wood substrates in boreal forests. Looking at the big picture is important for estimating the relative importance of different aspects and for evaluating the reliability of one´s results. To see the big picture, one may need to include also the tiniest study objects, being fungi or small dead wood sticks. To further broaden the view, one may also have to look beyond species identities and explore their traits. I hope that you got as curious about these subjects as I am, as I will dive deeper in the following chapters.

1.2 Dead wood and its fungal inhabitants

When walking in a natural forest, the most obvious structural element one literally soon "bumps" into is the plentiful dead wood in its different forms from standing trunks to grounded logs and branches. The lush results from

multiple factors starting from the variation in tree death: some trees die very slowly, first losing some branches and then gradually over the years losing all their life, while others are ripped from the ground with their roots by a storm. After death, a period of dead wood consumption by organisms follows as its chemical elements and nutrients are reused (Ausmus 1977, Franklin *et al.* 1987, Boddy 2001). Trees itself constitute from four different tissues - outer bark, inner bark, sapwood and hard wood. They all differ from each other structurally and chemically. Moreover, molecular elements of any tree tissues are cellulose, hemicellulose and lignin, all having their distinct structure. When all of this is combined with the chemical variation between tree species and decomposition processes, it is no wonder why dead wood serves a crucial habitat for thousands of forest-dwelling species (Stokland *et al.* 2012).

When kneeling down next to a log or looking closely a standing dead tree, one meets the leading actors of this thesis - the wood-inhabiting fungi, referring to all those species living as mycelium within dead wood or using it as a surface for attaching fruit bodies (Fig. 1). Majority of the species decompose different parts of the dead wood or dead fruit bodies of other fungi, being essential for nutrient and carbon cycles of the forests (Dowding 1981, Kahl *et al.* 2017). Those fungi that only utilize the dead wood as a surface for their fruit bodies are in a symbiotic relationship with trees as mycorrhizae. Many others have important role as parasites of other fungal species inhabiting dead wood. Some of the species even have special organs to capture nematodes to enrichen their diet (Peay *et al.* 2008, Stokland *et al.* 2012). All these species have also a crucial part in formation of new habitats and resources within the dead wood for other organisms. They, for example, affect the microclimatic conditions, change the structure of dead wood and their mycelium and fruit bodies are consumed by numerous organisms (Komonen 2003, Niemelä 2005, Schigel 2007, Boddy and Jones 2008, de Boer and van der Val 2008, Stokland *et al.* 2012). Thus, wood-inhabiting fungi are crucial part of the forest biodiversity as providers of ecosystem functions in boreal forests.

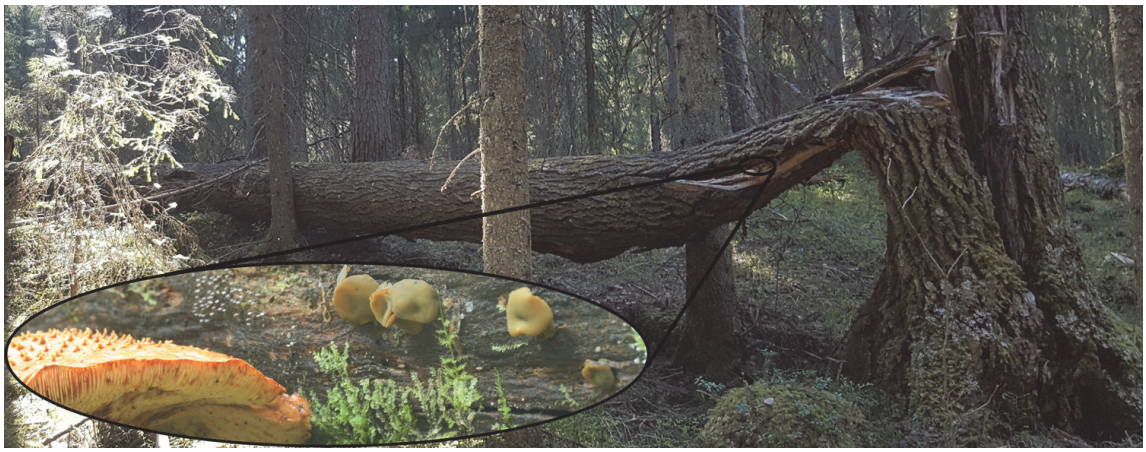

FIGURE 1 Wood-inhabiting fungi (*Chlorencoelia versifromis*, *Mollisia* sp., *Hyphodiscus "hemiamyloideus"*, *Lasiosphaeria* sp., *Orbilia* cf. *delicatula* and *Pholiota squarrosa* on a fallen log of European aspen (*Populus tremulae*) in an old-growth forest in Central Finland. Photo: Jenna Purhonen (the forest), Panu Halme (the fungi).

1.3 Methodological issues and detection problems

Optimal solutions for management and conservation of biodiversity require information that is not systematically biased (Niemelä 2000, Tyre *et al.* 2003, Field *et al.* 2005, 2007). Despite their undisputable importance in wood-inhabiting communities, majority of the fungal species inhabiting dead wood are still poorly known (Molina *et al.* 2011). Most studies in boreal Europe have included mainly polypores and corticioid fungi that produce large and long living fruit bodies, resulting in a biased view of the diversity of fungal communities on dead wood. In temperate Europe the situation has been improving recently as more and more studies have included also corticoids, agarics and even ascomycetes (Heilmann-Clausen and Christensen 2005, Abrego and Salcedo 2013, Bässler *et al.* 2014, Abrego *et al.* 2015, Baber *et al.* 2016, Krah *et al.* 2018). Still, especially species that produce very small fruit bodies (smaller than 1-5mm in diameter) have been neglected due to their poor detectability, difficulties in identification or lack of taxonomical information. For example, in the most recent Finnish Red-list, 67% of the more than 2000 non-lichenized ascomycetes were not evaluated due to poor knowledge (von Bonsdorff *et al.* 2010). In their study on ecological roles of fungal communities on spruce, Ottosson *et al.* (2015) were able to identify the nutritional strategy for ca. 60% of the detected Ascomycota operational units (OTUs), while the corresponding number for basidiomycetes was ca. 80%. The uncertainty was due to either that the authors could not find definite ecological information from literature, or they were not able to classify the detected fungi in adequate taxonomic level.

Due to its importance for biodiversity and forest functioning, dead wood has been incorporated into national monitoring programs and forest ecological and conservation science (e.g. Aakala 2010; Jonsson *et al.* 2016). Similarly as with wood-inhabiting fungi, there has been bias in a sense that the importance of small sized dead wood has been long overlooked. However, recently the importance of small dead wood for wood-inhabiting fungal communities has been acknowledged (Heilmann-Clausen and Christensen 2004, Juutilainen *et al.* 2011). Still, detailed information about dead wood profiles of forests are almost completely based on surveys considering coarse dead wood (diameter at breast height over 7-10cm, depending on the study) (e.g. Stokland 2001).

Another methodological issue worth considering arises from the detection problems of study objects. Detectability is defined as the probability of a study object to be observed if present at the survey moment (Garrard *et al.* 2008). Most often, if not always, detectability is less than one causing a problem of false-negative error, meaning a failure to detect study objects although they are present (Tyre *et al.* 2003). The problems that arise from this are manifold, for example, when assessing the conservation status of species, their extinction probabilities may be overestimated if their poor detectability is not accounted for (Kéry *et al.* 2006). Species vary in their detectability, depending on factors

like mobility, size, colour and growth type. Even the species-specific detectability may vary in time, space and depending on the study method (Tyre *et al.* 2003, Bailey *et al.* 2004, Kéry *et al.* 2006, Lõhmus 2009). Thus, solutions for tackling the problem also depend on the organism group in question. For plants, longer survey durations have proved to be more beneficial, while increased number of surveys per study sites was more efficient considering animals (Garrard *et al.* 2008). Considering fungi, it has been demonstrated that it is also matter of study questions, whether increasing the surveys in temporal or spatial matter gives optimal results (Abrego *et al.* 2016). The detectability problems of fungal species and dead wood pieces origin ultimately from different sources. For fungal species, the problem is more of a temporal kind whereas with dead wood it is spatial.

1.4 Drivers of species diversity in communities

Biodiversity is defined as variability of species between ecosystems and ecological entities, encompassing within and between species variability (Anonymous 1993). Humans are threatening and impoverishing biodiversity at an increasing phase (Ripple *et al.* 2017). In order to manage and conserve biodiversity successfully, we should have comprehensive understanding about the effects of different factors to survival and distribution of organisms (Simberloff 2004). In addition to knowledge about individuals and populations, we need information especially about communities, as only then the complex interactions between species can be accounted for. Communities are often the key unit in conservation and environmental problems (Townsend *et al.* 2003, Simberloff 2004).

A community is defined as "a group of interacting species populations occurring together in space"(Stroud *et al.* 2015). Ecologists have come up with hundreds of more or less different theories to explain the diversity and composition of communities (Palmer 1994). In order to clarify the situation, these theories can be regarded to explain community patterns based on four different main processes or their combinations, which are selection, speciation, drift and dispersal (Vellend 2010).

In practice, community ecological research has concentrated on observing patterns in nature, after which the undermining processes has been considered. Much attention has received the relationship of species diversity and area, disturbance or spatial heterogeneity, connection between local and regional diversity as well as temporal variability in communities during succession. The processes and their relative strengths are fundamentally system based and complicated to disentangle. Factors of which operative process is selection (i.e. biotic and abiotic interactions of organisms) has received most attention in research. Selection is considered the most important process in explaining the community composition, diversity and dynamics. Selection is effective when the species in a community differ in their fitness and it can be stable, depend on

density or vary temporally or spatially. The importance of speciation in community composition grows, when moving from local level to compare communities over environmental gradients or regions. Drift, i.e. stochastic variation in species abundances, on the other hand, is important process especially in small communities, but of course, the effect of stochastic events and change cannot be ever completely ignored. The effect of dispersal can only be considered together with the other processes, especially with selection and drift, when the dynamics of communities are affected by the size and composition of communities which between the dispersal happens (Vellend 2010, 2016).

1.5 Boreal forests and forest management

1.5.1 Forest stand

Forest stand dynamics include three basic processes: seed germination, tree growth and tree mortality (Terradas 2005). There are many physical (e.g. climate, disturbances) and biological (e.g. interactions between species) forces affecting these processes. In addition, all of these forces are in interaction with each other (Frelich 2002). The scene of my thesis is in the closed mesic spruce dominated forests of the southern and middle boreal zone (Ahti et al. 1968). In this system, forest dynamics is a slow process; trees are long living organisms and their decomposition takes many decades or even hundreds of years (Hofgaard 1993, Pretzsch 2009). The stand dynamics are commonly driven by small-scale tree mortality and by larger scale climatic events or disturbances, such as very cold winters, dry years, fires, windstorms or insect outbreaks (Spies *et al.* 1988, McCarthy 2001, Frelich 2002, Nilsson *et al.* 2004, Aakala *et al.* 2011, Komonen *et al.* 2011).

Humans with their management interventions greatly alter the natural stand dynamics in boreal forests (Kuuluvainen *et al.* 1996, Kouki *et al.* 2001, Kuuluvainen 2009). All of the three basic processes of forest dynamics are impacted. Natural tree germination is suppressed by planting monocultures and preventing natural forest renewal by effective fire control and lack of nurse trees (Lonsdale *et al.* 2007). Depending on the goals of the management, the natural tree growth is altered by manipulating the competitive relationships between tree individuals by thinning or selectively removing unwanted structures. Finally, early tree mortality is imposed with final harvesting by clear cutting or selective cutting (Lõhmus 2011). The overall change caused by human actions is the reduction and homogenisation of most of the structural features of a forest, such as tree age and size structure, as well as their spatial and temporal distribution (Kuuluvainen *et al.* 1996, Brūmelis *et al.* 2011). Due to these changes, a large number of species have become threatened in boreal forest ecosystems (Rassi *et al.* 2001, Siitonen 2001, Tikkanen *et al.* 2006). For example, in Fennoscandia, about half of the threatened species are associated to

forest (Tikkanen *et al.* 2006). Both deterministic and stochastic processes play their parts in explaining the observed effects and their importance depends on the spatial scale as well as what part of the change we are investigating (Vergnon *et al.* 2009, Chase and Myers 2011, Vellend *et al.* 2014)

In commercial timber harvesting the amount of dead wood in a forest is decreased from 40-170 m^3 per hectare typical for natural boreal forests (Aakala 2010), to less than 10 m^3 per hectare, in the worst cases 2-5m^3 per hectare (Siitonen 2001). Also, the dead wood profile of forests under management is changed via disappearance of very large diameter trees. For the overall biodiversity of the forests in Europe, dead wood related changes have been claimed to be the most influential (Esseen *et al.* 1997, Paillet *et al.* 2010). The negative changes simply relate to two interrelated theories, species-area and species–energy relationship, that include the interaction of speciation, drift and selection (Vellend 2016). These theories predict that with decreasing area and energy species richness decreases. On the one hand, this is due to the ability of smaller areas host less individuals than larger area and thus, just by chance, less species. On the other hand, habitat area also generally correlates negatively with decreasing habitat diversity, and thus less species with different habitat requirements can coexist (Arrhenius 1921, Wright 1983, Rosenzweig 1995).

As resources are removed, also the distance between dead wood pieces increases. In the theory of island biogeography, diversity of species decreases with area as communities experience more drift and with isolation as dispersal is more difficult (MacArthur and Wilson 1967, Vellend 2016). There are contrasting results on whether wood-inhabiting fungi suffer from poor dispersal abilities at the small spatial scales (Edman and Jonsson 2001, Komonen 2005, Kubartová *et al.* 2012, Norros *et al.* 2012, 2015, Komonen and Müller 2018). However in many studies the forest fragmentation and related dispersal challenges have been suggested to explain the observed declines in species richness (Stokland and Larsson 2011, Nordén *et al.* 2013, Halme *et al.* 2013).

Forest management may shorten the time (forest continuity sensu Nordén *et al.* (2014)) that the suitable habitats are available for species. The negative effect of this on species diversity can be understood via species-time relationship, that is a temporal parallel to species-area relationship, predicting that species richness increases with time. At short time scales the increase is explained by random processes such as incomplete sampling and year-to-year variation in the observed community from a static pool. At the longer time scales ecological processes such as climatic variability, community succession and population dynamics can cause the increase in species richness with time (Grinnell 1922, Preston 1960, Rosenzweig 1995, White *et al.* 2006). Species richness and also community composition of the forest stands is affected as species that are slow in their establishment, development or growth are known to suffer from poor forest continuity (Esseen *et al.* 1997, Fritz *et al.* 2008, Nordén *et al.* 2014). Also, species that require special habitats that only form during long time periods without disturbances are negatively affected (Niemelä *et al.* 2002).

In a long continuity, spruce dominated, natural forest where fire occurs seldom the microclimate is humid and stable (Esseen *et al.* 1997, Angelstam *et al.* 2004). Majority of the threatened red-listed fungal species in Finland are associated to this kind of shady coniferous forests (Tikkanen et al. 2006). This can be understood in the light of niche theory, that predicts species to differ in their environmental requirements (Vandermeer 1972). On the other hand, forest type interacts with the importance of microclimatic effects on species occurrence. For example, Junninen et al. (2006) concluded that the reason why in their study most fungi did not respond to changes in microclimate, and the species that actually were responding required open rather than shaded habitats, was that their study was confined to pine dominated forests. As pine forests are more open than spruce forests, it is logical that species inhabiting pine forests are more tolerant to wider variety of microclimatic conditions (Junninen et al. 2006).

1.5.2 Dead wood

Many of the dead wood characteristics are known to affect the community composition and dynamics of wood-inhabiting organisms. Many of the characteristics also correlate with each other, which leads into difficulties to disentangle their individual effects.

Decay stage of dead wood is one of the most important factors affecting wood-inhabiting fungal communities diversity and dynamics. As the time goes by, the fungal communities undergo succession from pioneer species to late decayers. Commonly species richness has been found to be largest in the intermediate stages, although red-listed species occur more commonly on more decayed trees over fresh ones (Bader *et al.* 1995, Renvall 1995, Lindblad 1998, Jonsson *et al.* 2005, Heilmann-Clausen and Christensen 2005, Ódor *et al.* 2006, Jönsson and Jonsson 2007, Arnstadt *et al.* 2016). However, the patterns that we detect by surveying the presence of fruit bodies do not always go hand in hand with the trends observed at the abundance or mycelial level (Sverdrup-Thygeson and Lindenmayer 2003, Ovaskainen *et al.* 2013). For example, an old forest indicator species *Phellinus nigrolimitatus*, thought to be restricted to well-decayed logs (e.g. Bader *et al.* 1995; Lindblad 1998), peaked its abundance and was found as a mycelium from a less decayed logs, indicating that only the fruit body formation of this species is restricted to late decay stages.

Continuity of the substrate may be important for species that are poor dispersers, colonizers or have slow establishment and growth rates (Fritz *et al.* 2008; Nordén *et al.* 2014). As described above with the stand continuity, the hypothesis of species-time relationship may have its role (White *et al.* 2006). The older the tree is when it dies the more different habitats it has. This is, for example, because when the tree gets older, some of its branches die before the tree dies. Thus, it would be expected that the more natural a forest is and the older the trees are, the more different habitats the decaying wood will host. This leads to a conclusion that logs in more natural forests should have more specialist species.

The consideration of different tree species in forest management often differs due to legislation or timber value. For example in Finland, the proportion of broadleaved trees in managed coniferous forests has been reduced by the forest management practices. Also, large ungulates are very effective in reducing their regeneration (Kouki *et al.* 2004, Edenius *et al.* 2011). Dead wood of different tree species differ in quality, the clearest distinction being between the groups of conifer and broadleaved trees. These tree groups share evolutionary distinct paths, and thus differ greatly by their structural and chemical characteristics (Stokland 2012a, b). Also, dead wood of different tree species differ from each other, for example in relation to the quality of bark, tree size, wood density, carbon concentration and chemicals inhibiting decay (Sandström *et al.* 2007, Rajala *et al.* 2010, Arnstadt *et al.* 2016). Host tree identity is known to affect fungal species richness and community composition (Rajala *et al.* 2010, Stokland and Larsson 2011, Hoppe *et al.* 2016, Kahl *et al.* 2017, Krah *et al.* 2018), and majority of wood-inhabiting fungal species in northern Europe are specialized to either conifer or broadleaved hosts (Stokland 2012c). Majority of the research conducted in the boreal region on wood-inhabiting fungi have considered conifer tree species, mainly spruce. An exception to this is a study by Rajala *et al.* (2010). They investigated fungal DNA on the four most common tree species that reach large diameters (aspen, birches, spruce and pine), and found that species belonging to Ascomycota constituted a higher proportion of the species on broadleaved trees than the conifers. Also very recently Ruokolainen *et al.* (2018) included aspen, birch, pine and spruce and found fungal communities to differ from each other between the tree species. In addition, deciduous wood, especially aspen, hosts a much larger proportion of red-listed species than what its relative abundance in boreal forests would suggest (Tikkanen *et al.* 2006).

As large diameter timber is the target of logging, this evidently changes the relative abundance of differently sized dead wood in the forests (Siitonen 2001, Eräjää *et al.* 2010). Size of the dead wood is well known to matter for wood-inhabiting fungi, especially to the threatened species (Nordén *et al.* 2004, Heilmann-Clausen and Christensen 2004, Abrego and Salcedo 2011, Juutilainen *et al.* 2011). Similarly as described above for area and energy at the forest stand level, with trunk size increases also the amount of available resources and space for attaching fruit bodies. Together with increased diversity of habitats, higher species richness can result simply because more species are able to coexist. Species richness may increase with size also because the chance of spores to land on a dead wood piece increases (Bader *et al.* 1995, Nordén *et al.* 2004). The community composition is also affected by the dead wood size. Especially for species that produce large fruit bodies, large amount of resource is required to fuel them. Larger dead wood also may host species that are specialized to more stable temperatures and moisture conditions. Fine woody debris (FWD) is also known to be important for certain species as the species composition between FWD and coarse woody debris (CWD) has been found to differ (Juutilainen *et al.* 2011).

Epiphyte and bark cover also affect community composition of wood-inhabiting fungi (Kubartová *et al.* 2012). Bark of a tree is a specific resource that inhabits species that are especially adapted to decay it or have some qualities that are required for species to use it as substrate to attach without using them as a resource (Kazartsev *et al.* 2018). Heilmann-Clausen and Christensen (2005) found a positive relationship between the species richness of wood-inhabiting fungi and the moss cover of the logs. They concluded the moss cover to indicate such microclimatic conditions that enhanced bryophyte but also fungal growth. Also, increasing moss cover might stabilise the microclimate of the decaying wood and thus advance fruit body production of wood-inhabiting fungi (Moore *et al.* 2008).

1.6 Traits - beyond species richness and composition

Mouillot *et al.* (2013) defined functional trait as "any trait directly influencing organismal performance". In addition to exploring the patterns of species richness and composition along environmental change caused by humans, a more in-depth understanding about the change in species communities and also in the ecosystem processes they provide, is gained when exploring the patterns of species functional traits in communities (McGill *et al.* 2006, Petchey and Gaston 2006, Mouillot *et al.* 2013, Vellend 2016). For example, in a situation where disturbance selects against specialized species but benefits generalists, there may not be change in the species diversity, but a decline in the functional diversity, that is the diversity of functional traits of communities (Petchey and Gaston 2006, Clavel *et al.* 2011). This is called also functional homogenization as communities that have relatively more generalists than specialists are assumed to have lower functional variability.

Fungal functional information and how environmental change affects the community functioning has been long neglected (Peay *et al.* 2008, Aguilar-Trigueros *et al.* 2015). The specialization of species often used in functional homogenization studies with plants and animals (e.g. Devictor *et al.* 2007, Abadie *et al.* 2011) is poorly known for most wood-inhabiting fungi (but see (Nordén *et al.* 2013). During recent years, however, studies with fungal traits has increased including ecological guilds (Ódor *et al.* 2006), trophic lifestyles (Bässler *et al.* 2014, 2016, Ottosson *et al.* 2015, Jönsson *et al.* 2016), decay type (Ruokolainen *et al.* 2018), and substrate preferences (Stokland and Larsson 2011, Juutilainen *et al.* 2017, Tikkanen *et al.* 2017). In addition, very recently a handbook aiming for standardising the trait measurement methods for basidiomycete fungi appeared (Dawson *et al.* 2018).

Studies including different guilds, such as lichens and saprotrophic fungi, have provided important insight into differences, but also similarities in the responses of groups differing in their nutritional mode to natural and human induced disturbances (Bässler *et al.* 2016, Jönsson *et al.* 2016). For example,

Jönsson *et al.* (2016) manifested negative effects of fragmentation and isolation on lichens while on decaying fungi there was no effect.

Traits relating to fungal fruiting have become a popular tool and subject of studies considering functional responses of fungal communities. Fungi produce fruit bodies for sexual and non-sexual reproduction. Spores or other dispersal particles are formed in the fruit bodies and dispersed to new locations. Sexual fruit bodies are the tool of this thesis for detecting fungal species inhabiting decaying wood, but their morphology and phenology is also the subject of study. Fruit body morphology and size has been used to disentangle the effect of anthropogenic and natural disturbances on fungal communities. Species with large and complex fruit bodies, such as perennial and pileate polypores, but also lichens, have been found to suffer from forest management, but benefit from natural disturbances that generate high amount of dead wood (Bässler *et al.* 2016, Abrego *et al.* 2017).

Among the species that produce fruit bodies, there seems to be high variation in the fruiting phenology, i.e. timing and longevity of fruit body production (Straatsma *et al.* 2001; Berglund *et al.* 2005; Halme and Kotiaho 2012). In addition to the differences between species, variation on the species-specific fruit body morphogenesis can derive from environmental factors, such as climate, temperature and nutrient and water availability (Straatsma *et al.* 2001, Gange *et al.* 2007, Moore *et al.* 2008, Kauserud *et al.* 2012). Also biological factors, such as disturbance and interactions with plant hosts or other organisms have been found to have an effect on fungal fruiting phenology (Moore *et al.* 2008, Violi *et al.* 2008, Dickie *et al.* 2010). Although the between and within species variation is acknowledged there has not been many studies about the species-specific fruiting phenologies.

Spore morphology has been included as a trait into several studies (e. g. Abrego *et al.* 2017; Calhim *et al.* 2018). An idea that fungi are good disperser over enormous distances, even from a continent to another, has been prevailing (Boddy 2008). However, recent findings have shown that fungal species with spores distributed by wind may encounter several dispersal obstacles. Generally as the spore size grows its dispersal distance shortens, but at the same time its fecundity probability grows (Norros *et al.* 2014). Also freezing and especially sun light are significantly affecting the dispersal success and may hinder the species ability to disperse in fragmented habitats or to habitat edges (Norros *et al.* 2015). Species-specificity to decay-stage has been found to increase as the spore volume decreased. This trend was observed in all of the wood-inhabiting fungal groups having different preferences to habitat species identity, from being generalists to single tree species specialist (Nordén *et al.* 2013). However, in previous studies in the temperate Europe, spore size did not relate to natural disturbance caused by bark beetle outbreaks, nor to the forest management and fragmentation (Nordén *et al.* 2013, Bässler *et al.* 2016, Abrego *et al.* 2017). Spore ornamentation has been suggested to facilitate the dispersal of ectomycorrhizal fungi via vectors (Hussein *et al.* 2013). Calhim *et al.* (2018) suggested ornaments to aid reaching lower soil layers via arthropod vectors,

while curved elongated spore shape was argued to be related to better attachment on the resource surface that experience precipitation.

1.7 The aims and importance of the thesis

My aim was to gain new information about the detection of fungal species and dead wood, their ecological importance, and to investigate the effect of forest management on them. As a whole, the thesis produces new information about biology of species, and how this can be used in conservation of the species and their habitat. This thesis begins with two methodological studies that deal with the two leading actors of the thesis, fungi and dead wood. These studies serve as a basis for the rest of chapters not only for their implications for methodology but for their insights on the ecology of organisms studied in these systems. The rest of the thesis concentrates on community ecological and conservation biological questions, including also the most poorly known wood-inhabiting fungal groups. Specific questions were:

1) When and how long different morphogroups fruit? (I)

2) What is the complete dead wood profile of a natural forest like? How sampling effort affects dead wood estimates? (II)

3) How does forest continuity and naturalness affect species richness and community composition of wood-inhabiting fungi inhabiting different dead wood species and types at different spatial scales? Are the responses different for different fungal groups? (III and IV)

4) How does tree species of the dead wood affect the functional composition of fungal communities? (V)

2 MATERIALS AND METHODS

2.1 Study sites

Depending on the study, there was from 1 (I and II) to 12 (IV and V) and 14 (III) mature study forests. All of the sites were situated in central Finland, in the southern or middle boreal zone (Ahti *et al.* 1968). The forest canopies were dominated by Norway spruce, accompanied with varying numbers of Scots pine, birches and European aspen. The ground layer was mosaic of *Myrtillus* or *Oxalis-Myrtillus* forest site types combined with smaller dryer, herb rich and/or mire patches (Cajander 1949). Illustrative photos of the forest structure of one study site, Kuusimäki, included in all of the studies are given in Fig. 2.

FIGURE 2 The forest structure of the semi-natural study forest, Kuusimäki. All photos are taken by Panu Halme.

Several different characteristics of the forests were measured to estimate the complete dead wood profile (II), naturalness (IV and V) or continuity (III) of the sites. The data for the age of dominating forest cover was received from Metsähallitus (IV, V). Number (II) and volume per hectare (II-V) or diversity of dead wood (III), and number of stumps per hectare (III-V) were estimated using different number of study transects or plots depending on the study. The type, tree species and volume of the dead wood was recorded and decay stage was estimated. Shannon's diversity index (H) (Shannon and Weaver 1949) for the dead wood was calculated, using dead wood types based on their dead wood category, canopy position and decay stage (III).

Canopy openness around each study log was estimated using photo taken with fisheye lens to all of the four principal compass directions (III). ImageJ program was used to estimate the proportions of visible sky from the photos, and a mean of the four proportions was then extracted (version 1.45s; Schneider *et al.* 2012).

2.2 Study logs for fungal surveys

For all of the study logs, tree species identity, decay stage and volume (IV and V) were recorded and estimated as described above for site level dead wood data. The diameter at breast height was measured to account for survey effort instead of log volume (III). Percentage of bark (III, IV, V), lichens (III), and moss (I, IV and V) covering the log surface was estimated visually.

Dendrochronological methods are widely used in the research of forest dynamics, where the dating of tree rings, ring widths and other ring features has been used to reveal past forest disturbances and ecological events (Fritts and Swetnam 1989, Lorimer and Frelich 1989, Frelich 2002). In this thesis (III), these methods were used to gain detailed information about the continuity of the study substrate; the dead standing pines. The dating was done from cross-sectional sample discs of the study logs. Site-specific marker years were obtained from the master chronology built using the increment cores of live trees close to the study logs (Yamaguchi 1991). WinDENDRO software (Regent Instruments Inc. 2015) was used for measuring tree widths visually, and confirmed statistically with COFECHA-software (Holmes 1983). After the year of recruitment and death for each study was estimated, the age at death (ADD) was simply the difference of these years, whereas the years from death (YFD) was the difference of the sampling year (2015) and death year.

2.3 Fungal surveys, nomenclature and traits

All fungal occurrence data were based on thorough observation of the substrate for sexual fruit bodies. All other fungal groups were included but lichenized fungi, except that lichen genus *Micarea* was included (III). The logs (I, IV and V) were surveyed completely, while the standing pine trunks (III) were carefully inspected up to the height of 1.8 meters from the ground. In study I, twelve repeated surveys were conducted for each of the study logs, while the amount of surveys was one in study III, except for agarics two, and in studies IV and V two for all groups of fungi. The surveys were conducted during the years 2010-2014, the first surveys performed in May and the last in October.

If it was possible, each fungal occurrence was identified to the species level in the field, but most often a sample had to be collected for later identification in the laboratory with a 1000 times magnifying light microscope.

If a species level identification was impossible a highest taxonomical or morphological group status was given and groups were separated with numbers (e.g. pyrenomycete sp1., sp2., etc.). Several identification guides and species experts/taxonomists were included in the identification of species. The identification of polypores was mainly conducted by Anni Rintoo, discomycetes by me and Seppo Huhtinen, pyrenomycetes by Thomas Læssøe and me, *Micarea* lichens by Annina Launis, calicioid fungi by Hanna Tuovila, majority of the corticioids by me, Heikki Kotiranta and Jorma Pennanen, genus *Piloderma* by Matti Kulju and tomentelloid fungi by Nerea Abrego. Panu Halme was responsible of agarics and tremelloids. Majority of the utilized literature are reported in Appendix 2, V.

The nomenclature of fungal species followed Index Fungorum (Royal Botanic Gardens Kew *et al.* 2015 for I and 2016 for III, IV, V). For *Micarea* species it followed Coppins (1983), Czarnota (2007), and Czarnota and Guzow-Krzemínska (2010), and for *Mycocaliciales* species Tibell (1999).

The detected fungal species were categorized into different morpho-groups based on visual inspection of their fruit body morphology (I, IV and V). The following grouping was used in study IV; 1) agaricoid (fungi with soft pileus and stipe as well as pleurotoid fruit bodies without stipe, hymenial layer lamellae or smooth), 2) discomycetoid (hymenial layer in disc- or cup-like structure), 3) pileate (when mature, most of the fruit body forms a hard pileus or is erected on the edges, but at first grows as crust on the log surface), 4) pyrenomycetoid (hymenial layer inside peritechial structures, not embedded in stromatal layer), 5) ramarioid (hymenial layer on branched structures), 6) resupinate (most of the fruit body appressed to the substrate with exposed hymenium, can be slightly erected or pileate on the edges), 7) stromatoid (hymenial layer inside perithecia embedded in stromatic tissue), 8) tremelloids (jelly-like fruit body). The grouping slightly differs from the above in study I and V, for example in study I the perennial and annual split of polypores was based on Niemelä (2005). In study III, the distinction was done based on nutritional mode, other fungi being decayers, and *Micarea* lichens treated as a separate group from them. Majority of the information of spore-related traits was gathered from the identification guides and specific publications mentioned above (V). For taxa that the species level identification was not possible or data were not available, I visually observed the traits. For spore size, always three spores were measured while inspecting the sample under the microscope for their length and width and a mean from these was then extracted. If more than one collection per taxa were made, a mean from the means were extracted for the analyses, thus there is no within taxa variation in the traits.

2.4 Analyses

All descriptive illustrations and analyses in this thesis were performed using the program R (R Core Team 2015, 2016, 2017). To test whether there was difference in fungal fruiting longevity between different morphogroups (I), or species richness between host tree species (V), Kruskal-Wallis one-way ANOVA and Nemenyi pairwise comparisons were used.

Randomized sampling loop was built to explore the effect of sampling effort on the estimated number of dead wood items per hectare of different tree species and their coarse and fine fractions (II). First, a fixed number of study plots, ranging from 1 to the total number, were randomly selected among the total plot pool. A mean number of dead wood items per hectare was then calculated based on the selected plots. The sampling for each number of plots was repeated for 1000 times.

Randomized species accumulation curves were constructed in order to compare the species diversity difference between logs in seminatural and natural forests (IV) and of different host tree species (V) using "Specaccum" function in the "vegan" package (Oksanen *et al.* 2017).

Generalized linear models were used to study the relationship of site level species richness and environmental variables (IV), while generalized linear mixed models were used to study how environmental variables explained the species richness at the log level, simultaneously accounting for the hierarchical random effect of the site identity (III and IV). In all models, the species richness was assumed to be Poisson distributed, and logarithmic link function was used. Function "glmer" of the package "lme4"(III, Bates *et al.* 2016), and function "glmmTMB" of the package "glmmTMB" (IV, Magnusson *et al.* 2017) were used for modelling.

Nonmetric multidimensional scaling was used to illustrate the effect of environmental variables on the community composition (III and IV). The number of dimensions was selected based on the stress level that was set to be under 0.2, thus two to four dimensions were selected depending on the fungal group. Function "metaMDS" was used with Bray-Curtis dissimilarities of each of the community pairs. To disentangle the best variable or combination of variables explaining the community composition, Spearman rank correlation analysis between community dissimilarities and different combinations of the Euclidean distances of scaled explanatory variables were conducted using function "bioenv". Both of the above functions are from the "vegan" package (Oksanen *et al.* 2017).

A Hierarchical Modelling of Species Communities (HMSC) that is operationalized as a hierarchical Bayesian latent-variable joint species distribution models, utilizing generalized linear mixed models (Ovaskainen *et al.* 2017) was used to explore the effect of environmental variables and substrate quality on the trait composition of fungal communities (V).

3 RESULTS AND DISCUSSION

3.1 Fruiting phenology of wood-inhabiting fungal groups (I)

There was a great variation in fruiting timing and longevity both within and between different morpho-groups of wood-inhabiting fungi. The between group differences were mainly due to agarics, fruiting significantly later and shorter than other morpho-groups. In previous studies, soft and projecting nature of agaric fruit bodies was concluded being more affected by abiotic and biotic factors such as water availability and predation than, for example, perennial polypores (tough, woody) which may be visible for a long time prior and post spore production (Schigel 2007, Halme and Kotiaho 2012). However, as here the whole fruiting period of occurrences were monitored, often constituting of many fruit bodies and ongoing wilting of old and production of new ones. Thus, in the present case the combined effect of seasonally late timing of fruiting and the beginning of winter (sudden break down of all fruit bodies) was probably the main reasons for the consistently shorter fruiting of agarics.

Most morpho-groups did not differ from each other significantly considering their fruiting phenology. This was partly caused by the large within group variation of the traits. There are several potential reasons for this phenomenon. First of all, the morpho-groups are generally phylogenetically diverse (Hibbett *et al.* 2007), so a shared fruiting phenology was not ancestrally shared among all taxa within each group (Hibbett *et al.* 2007). Secondly, the morpho-groups also consisted of species that differ from each others in relation to their roles in the community or their requirements of microhabitat within a tree trunk. For example, within corticioids most species were decayers, while some were symbionts (e.g *Tomentella* sp.), parasites (e.g. *Stereum rugosum*), and even predators (e.g. *Peniophorella praetermissa*) (Kotiranta *et al.* 2009, Stokland *et al.* 2012). Some of the species might be specialized to decay thin branches still attached to the large logs, whereas some others decay large logs and are able to produce fruit bodies only after several years of resource gathering (Ovaskainen

et al. 2013). The variability in these species-specific characteristics is likely to be reflected in fruit body morphologies and fruiting phenologies.

Several species had also high within species variation in their timing of fruiting. It might be that these species are opportunists, i.e. able to produce fruit bodies whenever they have enough energy and somewhat suitable conditions. Also, species that produce fruit bodies late in the season, overwinter, and start to produce spores early in the spring, seemed to have large variation as they were often spotted in the early season and late season but not in between. This might explain high variation considering for example *Humaria hemisphaerica*.

The species-specific data must be, however, dealt with caution since the study was relatively small and covered only one growing season. Only few taxa were common on the study trunks, while 70% (167) of the taxa was detected on only one or two study trunks. A small number of study trunks is obviously explaining most of this pattern but it is also consistent with earlier studies showing that there is a high species turnover on fungal communities already on short distances (Abrego *et al.* 2014). Thus, long term studies would be needed to fully differentiate the effect of environmentally and biologically induced variation in species-specific fruiting phenologies.

3.2 Dead wood in semi-natural boreal forest (II)

The estimate for FWD in the forest massively outnumbered CWD when it came to the richness of dead wood pieces (31 million over 58 thousand per 108 ha), while CWD accounted majority of the dead wood volume in the forest (97%). However, there were clear differences between different tree species. For spruce, the pieces < 1cm at diameter formed 99% of the dead wood richness, while for aspen the number was 63%. Also, the decrease in the richness as the diameter increased was very abrupt for spruce but more gradual for aspen. An important practical conclusion that follows is that the total dead wood amount of a forest is not necessarily a universally valid proxy of its conservation value for fungal species with different requirements (Juutilainen *et al.* 2017). For example, for generalist species inhabiting FWD the forest offers millions of suitable resource units and thus the population sizes for these species may be enormous, while for species that have very specific resource preferences the population sizes would be much smaller.

The slash and burn history of the study forest was differently visible in the dead wood profiles of different tree species, in which the dead wood was divided into decay and diameter classes. Birch constituted more than 50% of the forests total dead wood volume. This result was very logical, as being a fast growing pioneer species, birch has been very abundant in the canopy after the cultivation had stopped in the 1860s. The peak in the volume of largest logs (>40cm in large-end diameter) of decay stage three and a drop in volume in the decay stage two may partly result from that the time frame for birch in decay stage three is relatively longest. This result also indicates, that in the future the

amount of birch dead wood will drastically drop as the regeneration of birch has been very low during recent decades in the absence of stand replacing disturbances (Linder *et al.* 1997). Aspen, also being a pioneer tree species, shares the same fate as birch, but its dead wood peaked at the decay stage two. This difference might be caused by the longer average lifespan of aspen when compared to birch (Tikka 1954, 1955). These trends are problematic as the forest is currently hosting several threatened aspen and birch inhabiting fungal species with high population sizes and is the only known locality in central Finland (Halme *et al.* 2018 (in prep)). For spruce on the other hand, being a late successional species, the cultivation history is probable to explain why very large (>40cm base diameter) decaying logs are still lacking from the forest but are likely to increase heavily in the future.

Self-thinning and competition might explain why birch, spruce and pine were relatively well-presented in the intermediate diameter classes. For aspen there was a clear cap in these classes, and this might be due to that the regeneration of aspen is probably further hindered due to browsing pressure from large herbivores (Kouki *et al.* 2004, Edenius *et al.* 2011). While the more even abundance of 2-19 cm diameter aspen dead wood was likely to result from regularly falling large braches typical for aspen. As a conclusion, the dead wood profiles of different tree species tell a tree species-specific story as they differ greatly for their ecology and life history traits, which should be taken into account when estimating the dead wood continuity of forests based on dead wood profiles.

3.3 Forest continuity and naturalness (III and IV)

The species richness of neither of the studied guilds (decayers and lichens) had a significant response to forest stand continuity, measured as the dead wood diversity (continuity increasing) and number of stumps per hectare (continuity decreasing). However, there was a positive relationship of *Micarea* richness to the continuity of the microhabitat, measured as the time since the tree death while for decomposers there was none (III). On the other hand, the forest stand naturalness, measured as total dead wood volume (naturalness increasing) and number of stumps (decreasing) per hectare as well as the age of the dominating tree canopy (increasing) had a positive, but weak, relationship with the overall wood-inhabiting fungal species richness. When investigating the morpho-groups separately, the response was mostly due to discomycetoids and pyrenomycetoids on pine (site level) and pileates on spruce (log level). For majority of the morpho-groups there was no significant relationship of any kind (IV).

The reason for observing only weak or no trend in species richness along forest stand quality gradients resulted from multiple factors. On the other hand, species interactions in the form of, for example, competitive exclusion may have prevented linear increase in species richness with increasing continuity and

naturalness in the case when more competitive specialized species replace generalists (Nordén and Appelqvist 2001, Heilmann-Clausen and Christensen 2005). This hypothesis is supported by the observed increase in the community similarity of both *Micarea* lichens and decomposers with decreasing dead wood diversity, possibly resulting from forests with lower stand continuity having more shared generalist species (III).

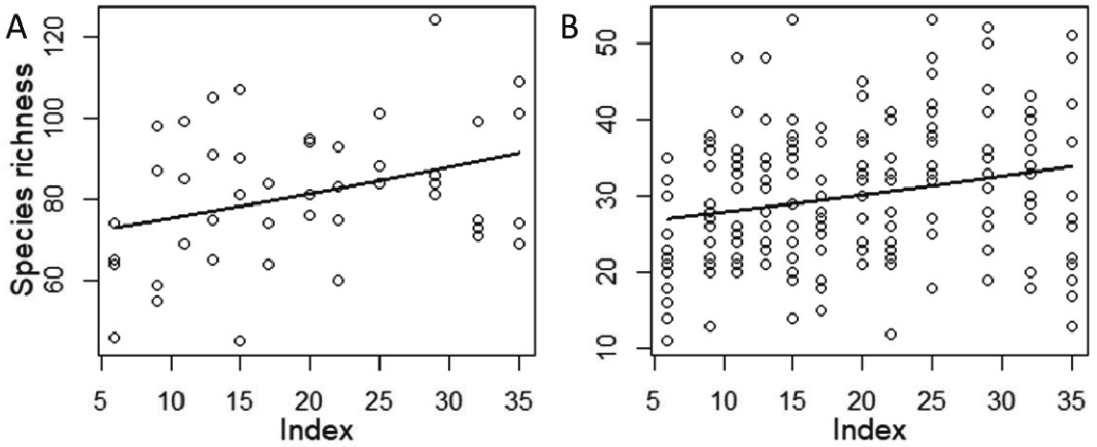

FIGURE 3 Fungal species richness in relation to forest naturalness index at A) site level, and B) substrate level. The line represent linear regression (IV).

On the other hand, pine-inhabiting fungi have been suggested to be better dispersers and less affected by disturbance and microclimatic variation than species inhabiting spruce. This is because natural pine forests are subject to frequent forest fires, their microclimate is more dry and structure more open as well as they have lower input rate of dead wood than spruce forests (Angelstam 1998, Junninen *et al.* 2006, Stokland and Larsson 2011). The weak relationship of forest continuity and naturalness with species richness may thus also indicate that most studied groups are not dispersal limited at the forest stand scale. These results are in accordance of several previous studied that also did not find a connection between stand continuity and species diversity (Groven *et al.* 2002, Sverdrup-Thygeson and Lindenmayer 2003, Rolstad *et al.* 2004).

Still, the site level positive response to forest stand naturalness was mostly caused by fungal groups inhabiting pine (IV). This was likely to result from higher variability in the volume of the studied pine dead wood in the most natural sites compared to the least natural sites. This was probably caused by the fact that pine continues growing in diameter also when the tree gets really old (Agren and Zackrisson 1990), and thus largest pine logs were only encountered in the most natural sites. Pine also naturally dies very slowly, during which it comes very decay resistant kelo tree. Kelo trees are known to host specialized species and thus the site level species richness is higher for forests with both kelo dead wood and pine dead wood of some other quality (originating e.g. from self-thinning) when compared to forests that lack kelo dead wood (Niemelä *et al.* 2002, Stokland *et al.* 2012). In addition, the proportion

of kelo pines is logically highest among the oldest pine trees. As kelos are inhabited by a limited number of specialized species, this might explain why the species richness of neither of the studied guilds responded to tree age at death (III).

Positive response of *Micarea* lichens and pileate group inhabiting spruce to forest continuity and naturalness, respectively, is most probably because these groups suffer from colonization and establishment challenges. Previous studies have concluded the increased time for colonization to be important for lichens (Johansson *et al.* 2007, Fritz *et al.* 2008). While in their review about dispersal ecology of wood-inhabiting insects and fungi Komonen and Müller (2018) argued the colonization and establishment be more important factors causing negative responses to forest management than dispersal, per se. The different responses of groups might be explained by the fact that crustose lichens are consistently characterized by having slow establishment and growth rate (Stenroos *et al.* 2011, Nordén *et al.* 2014), while the decomposers as a group was found to be more heterogeneous including contrasting species-specific responses (III, Supplementary data 2). In addition, for lichens competitive exclusion is suggested to be rare (Lawrey 1991, Uliczka and Angelstam 1999) and thus they would be expected to respond to continuity as predicted by the species-time relationship (Rosenzweig 1995, White *et al.* 2006).

However, it is important to remember that the sites with lowest continuity and naturalness in the landscape were not included into the studies as they lack the substrate the studies were targeting. For example, here the average amount of dead wood per hectare was as high as 60 m^3 per hectare in the least natural sites IVI. In addition, the sites with the highest management intensity (III) had four to five fold less stumps per hectare as, for example, Penttilä *et al.* (2004). Thus, the present conclusions about the overall importance of forest naturalness or continuity for most species groups must be considered with care.

3.4 Host tree species (IV and V)

The species richness was higher on broadleaved than coniferous dead wood (V). Not many studies have compared the species richness of different tree species, but this result is logical when considering the chemical differences of broadleaved and coniferous trees. Due to their more effective defensive chemicals such as resin, coniferous dead wood is more difficult to decay which may lead to lower species richness when compared to broadleaved dead wood (Stokland 2012b, c).

The community composition was mostly explained by the dead wood tree species being either broadleaved or conifer tree, and communities in spruce and pine being more different from each other than those in birches and aspen (IV). Dead wood tree species comprised 71% of the variation that was explained by the model on species occurrences, compared to 5% explained by the forest naturalness (V). These results are in accordance with previous studies on the

importance of tree species of the dead wood driving the community composition, and being even more important than forest management (Rajala *et al.* 2010, Kahl *et al.* 2017, Krah *et al.* 2018, Ruokolainen *et al.* 2018).

Fruit body morphology predicted the specialization of species to different dead wood species. Species with discomycetoid fruit body were specialized generally to broadleaved dead wood, while pyrenomycetoids were specialized to birches in particular. Resupinates were conifer generalists, while pileates were specialized to spruce. The fungal communities had on the average larger and more elongated spores on broadleaved and larger dead wood and smaller and more spherical spores on coniferous dead wood (V). These results indicate the strong selective effect of dead wood quality that is visible not only at the species diversity but on their traits. The underlining reasons may relate to species evolutionary strategies or interaction between traits. For example, the spores of pyrenomycetoid fungi were largest and most elongated. The results are also in line with the study by Bässler *et al.* (2014), in which they suggested that species with smaller spores follow *r* strategy and thus their proportion in the community is higher on smaller dead wood.

3.5 Methodological insights

3.5.1 Poorly-known fungi (I, III, IV and V)

This thesis clearly shows the importance of including different fungal groups and spatial levels in a shared study setup in conservation biological research. Taking into account the number of detected species that were: 1) not yet described to the science, 2) new species to Finland (couple of examples published in von Bonsdorff *et al.* 2015; von Bonsdorff *et al.* 2016), and 3) number of group-species, I can conclude that great deal of wood-inhabiting fungal species in boreal forests constitutes from poorly known species. These species belonged mainly in resupinate morpho-group or in the phylum Ascomycota. Despite the relatively small sample size, species like *Phlebia bresadolae*, classified as regionally extinct in Finland (von Bonsdorff *et al.* 2010) and *Tulasnella cystiophora* previously recorded 200 years ago were rediscovered (Kotiranta *et al.* 2009).

A clear example about the effect of methodological decisions on results can be made for species belonging to Ascomycota. If the lower size limit of 1mm for fruit bodies would have been used to include species into the study I (Abrego and Salcedo 2014, Abrego *et al.* 2017), about 50% of the species belonging to Ascomycota would have been neglected (I). With lower size limit of 10mm, as for example in Heilmann-Clausen and Christensen (2005) and Ódor *et al.* (2006), only 12% of the detected Ascomycota would have been included. Unfortunately, these comparisons had to be made with studies conducted in the temperate areas as no community ecological study based on fruit body data has included Ascomycota of any size in the boreal regions.

The results on agaricoid and ramarioid fungi are with most uncertainty (IV and V). Although the agaricoid richness was large in total, they are the most ephemeral when it comes to their fruiting (I). For ramarioids, the species richness was low and most logs were empty. However, this group included many poorly known species, and thus surveys should be made to specifically plan the study setup to serve this purpose. For example, an endangered *Clavicorona cristata* was found in one of the study pines, the second known locality in Finland. At the moment there is no proper information about why this species is so rare.

3.5.2 Detection of wood-inhabiting fungi and dead wood (I and II)

Perennial polypores were fruiting throughout the season and are potentially well detected by one survey conducted at any time during the growing season (e.g. Halme and Kotiaho 2012). This is not surprising since they have durable, woody fruit bodies. The detectability of perennial polypores may thus be mostly affected by the fact that many of these species can be active in trunks for a long time before they start to produce fruit bodies and not so much by their yearly fruiting phenology (Ovaskainen *et al.* 2013).

Many annual polypores and corticioids had a relatively long fruiting longevity, i.e. they basically fruited through the whole season. At least half of the fruiting taxa of these morphological groups would have been detected by a single survey at any time of the season. However, also taxa with shorter fruiting longevity exist in these groups and new taxa were accumulating constantly as the study period exceeded. Thus, one survey in the early season and one in the late season would better allow detection most fruiting taxa of these groups. In addition, most corticioid species were already fruiting at the first survey. Instead of claiming most corticoids being spring fruiters, we think that the fruit bodies could have been present from previous season and are most likely perennial similarly as many polypores growing new hymenial layer on top of the old hymenium from the previous year. Longer monitoring studies would be needed to reliably answer to this question.

On average, discomycetes had a fruiting longevity of nearly two months, which is longer than was expected. For pyrenomycetes the observed long average fruiting longevity (somewhat less than three months) is not that surprising since the hard peritechial fruit bodies of pyrenomycetes are very durable, and thus once produced stay visible for a long time even after the spore production has ceased, possibly for several years. The taxa of disco- and pyrenomycetes were accumulating fast in the early season levelling to a constant accumulation speed for the rest of the study period. However, the small number of taxa detected for these groups during the first sampling occasions is probably partly resulting from the untrained eye of the surveyor, not able to detect the taxa even though they were present since many of the species in these groups are very small. Thus, more reliable accumulation curve would be more linear, resembling the curve of annual polypores and corticioids. This means that the above-mentioned guidelines for annual

polypores and corticioids apply also for pyrenomycetes. For discomycetes, more surveys are needed to reach similar detection level, since their fruiting longevity is clearly shorter than that of annual polypores, corticioids and pyrenomycetes. The fruiting of the discomycetes and pyrenomycetes, both constituting from species belonging to Ascomycota, did not level down towards the end of the season, and for discomycetes, it actually increased firmly. Thus our recommendation is that also Ascomycota species are surveyed along the whole season instead of focusing at spring time (e.g. Nordén *et al.* 2004).

Heterobasidiomycetes and agarics had the shortest average fruiting longevity. Heterobasidiomycetes were accumulating at a constant speed during the whole study period. Especially resupinate heterobasidiomycetes appear right after the snows have melted, and are fruiting the whole growing season, but they are very difficult to detect during the dry summer months (Heikki Kotiranta, personal communication). The fruiting of agarics had the most seasonal pattern of all the groups, with most taxa producing fruit bodies after the summer months. These results indicate that the detectability of these groups is lowest compared to the other groups and a guideline for their sufficient surveying for would be to conduct several surveys, as recommended also by Halme & Kotiaho (2012) for agarics and emphasize them towards the late season. It is natural, that for groups in which timing of fruiting was emphasized towards the end of the season, such as agarics and heterobasidiomycetes, the fruiting longevities must be shorter than for groups fruiting earlier. In addition, for agarics the start of snowing is more likely to be also the true end of the fruiting season, but for heterobasidiomycetes the true end is more inconstant, since fruit bodies with gelatinous tissue of extracellular colloidal material is argued to be less disturbed by freezing than fruit bodies with more precisely orientated cell. Many discomycetes also obtain similar gelatinous structure (Sherwood 1981). The start of the winter season in Finland is also varying, since the snow can melt many times before the permanent snow settles.

Applying group level information of fruiting phenologies (the timing and longevity of fruit body production) provides insights for better understanding of fungal communities and for performing fruit body surveys with optimal methods for different morphological fungal groups. Yet, the variation of these traits remains large when the groups in consideration are morphological such as corticioids, discomycetes or agarics. If the species-specific fruiting phenologies are not taken into account, there is a danger of having a skewed estimation of species abundances, for example in fungal conservation efforts. On the basis of similar fruiting phenology data as seen here (I, Appendix 1), a correction factor for different fungal species could be calculated in a similar manner as the basal detectability adjustment calculated by Järvinen and Väisänen (1975) for correction of the breeding population size for birds in line transect censuses. The data of study I is constrained temporally and spatially, hence, more detailed fruiting phenology surveys covering multiple years as well as climatic zones are needed in the future to confirm the findings and also include other fungal groups than wood-inhabiting fungi.

When conducting dead wood sampling using 10 m x 10 m study plots, different number of plots were needed to gain reliable estimates of different tree species, that is to avoid overestimating or not detecting the specific dead wood in question. More rigorous sampling was needed for tree species that had a clustered growth style or were rare in the forest, being aspen and pine respectively in the present study, while birch and spruce were the opposite. For aspen, that grows in clusters due to its clonal regeneration (Shepperd *et al.* 2001), about 50 sampling plots were needed to avoid false-negative estimates for both FWD and CWD. For making a more overall estimation of the total dead wood of the area about ten randomly distributed plots should be sufficient.

3.6 Conclusions for conservation

Most importantly, this thesis demonstrates the importance of treating fungal groups separately in conservation management and planning. The conservation guidelines, provided by Junninen and Komonen (2011) considering polypores stating that the minimum amount of dead wood 20m^3/ha, should be updated. Here the negative effect of forest management was still visible in pileate morpho-group (consisting mostly of polypores) inhabiting spruce although the amount of dead wood was on the average about 60m^3/ha even in the least natural forests. On the other hand, for other morpho-groups these semi-natural forests hosted similar diversity as the most natural sites having circa twice the dead wood.

Also considering different tree species separately is important, as they host different fungal communities and are important for different fungal groups for different reasons. This thesis highlights the importance to target for diverse tree species composition in fungal species conservation for preserving diverse wood-inhabiting fungal communities

Pine is a very special case among the tree species of boreal forests as the period for dynamics of pine trees from germination to total decomposition is a millennium rather than centuries. Thus, its consideration in forest management is very difficult and should be more addressed.

Acknowledgements

I have been very lucky to have so many amazing people supporting my way to survive the PhD and the rollercoaster of life. First, I want to thank my three supervisors. Panu, it is hard to find the words that would describe well enough my gratitude and appreciation to you. You are the reason why I did this PhD. You were the first friendly and accepting person that I remember, when I first time entered the department, and since then you have been an important role model for me. Thank you so much for believing and trusting me, being also strict and pointing openly the weak points where I need to improve to be able to finish this thesis and advance to be a scientist. All in all, it has been a privilege to have you, not only as my supervisor but as a role model, teacher and friend, thank you so much. Atte, your role as my supervisor grew towards the end of the project and was essential for me to be able to wrap things up. I really admire your way to work and do science, and it has been very educating for me to learn from you. Thank you so much for being there for me! Seppo, you have been a great teacher of all fungi to me, but most importantly of discomycetes. Besides being my great teacher, you have been a great friend as well. Thank you for sharing your expertize and friendship with me.

I feel that this thesis is really a great example of successful teamwork. Special thank you for all of my co-authors! Including all of the most poorly known fungal groups was maybe a bit ambitious, but luckily, I received a lot of help during the data collection. Thank you Nerea, Panu, Noora, Katja, Meeri, Nasu, Sandra, Titta and Steve for those moments in the forest. Surviving the exhausting fieldwork together with listening to my personal problems must have been quite tough for you. Also, thank you Leena for the help with collecting the trait data from the literature, and Panu Kuokkanen from the Metsähallitus for providing the information about the study sites. I was also lucky to get help from the best species specialists in Finland and Europe. Katja, Heikki, Jorma, Matti and Nerea thank you for teaching me and helping with identification of corticioids. Seppo, Thomas, Unto, Timo, Hanna and Annina, thank you for teaching me and/or identifying the ascomycetes and lichens. Anni, thank you for identifying the polypores, and Panu, Meeri and Sonja for identifying the polypores, agarics and heterobasidiomycetes. Thank you Tuomas for introducing the secrets of forest dynamics and dendroecology to me already at 2011 in Sweden. Finally yet importantly, being able to include the freshest analytical methods I am most grateful to you, Nerea and Otso, for the work with HMSC.

In the beginning of this project, I spent, not many days or months but years in the basement of the Natural history museum of Central Finland identifying the fungi from the dried samples. The personnel working at the museum were super! Thank you Jyrki, Jonna and Tanja among others for your company and tolerance for me taking all the coffee mugs or singing very loudly the whole day. In addition, our basement gang was fierce, thank you creeps and Panu for the moments below the ground.

The process for coming a young scientist has been quite a slow one for me. I am very thankful for various people, projects and networks that have helped me to build my identity as a researcher. Several strong women have showed me the way and been great role models for me; Katja, Anni, Noora, Nerea, Anna and Kaisa R., thank you for teaching me so much! It has been also a luxury to belong to the greatest research group in the world: the Intervention Ecology Research Group. I also want to thank all of my teachers and colleagues at the department, you all have made the working atmosphere very nice and cosy. At the department, I have been situated in two different offices. The first office I was sharing with Piret, Inka, Jaakko, Jaakko and Guille. I feel that the researcher in me was born in that office during the discussions and group works with my officemates. Then began the era of the "Pieru-office", which has been very important for the maturation of the researcher within me to reach the point where I am now. So thank you Eini, Ilona and Kaisa R. I am also grateful to my master student Mari Jäntti, all of my students I have taught, and all the people in the Monday Coffee Club, the board of the doctoral programme, the wonderful team of ECCB 2018, the NEFOM network and Jyvässeudun Sieniseura ry for all of the collaborations, trust and support I have received.

I also received very useful advice and financial support during this project. I wish to thank my follow-up group members Mikko Mönkkönen, Saija Kuusela and Heikki Kotiranta for your advices and constructive suggestions during our yearly meetings. You always managed to give me more vigour to continue. Great thank you for the preliminary examiners Olli-Pekka Tikkanen and Anne Sverdrup-Thygeson for very positive feedback and valuable suggestion to improve the thesis. I am very honoured that Mari Jönsson agreed to be my opponent. I am also deeply grateful for the Ministry of Environment, the Finnish Foundation for Nature Conservation, the Finnish Cultural Foundation and the Doctoral Programme in Biological and Environmental Science of Jyväskylä University for funding this thesis.

A big influence for getting excited about fungi in the first place belongs to the people of the "fungal family". Already at 2009, when I first time went to the national extended fungal course, I was surrounded by people with so much enthusiasm towards fungi, it is beyond imagining, and at the same time I felt really like home. Also, a special thank you to Tea von Bonsdorff and everybody else working in the Specialist Group for Fungi for being so welcoming and allowing me to participate the inventories and helping with the newest threat assessment. Thank you so much my whole "fungal family" for all of the lessons, enthusiasm, saunas, dancing and karaoke!

Ensimmäiset neljä kouluvuottani sain suureksi etuoikeudekseni viettää Oravasaaren kyläkoulussa, metsän keskellä, männikkö mäellä. Arvostukseni ja kiinnostukseni luontoa kohtaan kasvoi ja sai tukea tuona aikana. Saimme luontokirjat, hienot sveitsiläiset linkkuveitset ja kenttäkeittoastiat, joita käytimme Jaakko-opettajan viedessä meitä luontoretkille, milloin minnekin. Jaakko ja Sirkka Palmu, kiitos teille parhaasta mahdollisesta koulutien alusta mitä ihminen saattaa toivoa ja kipinästä luonnon arvostukseen.

Family and friends are the most precious things in my life. Sharing the good and the bad moments together has been crucial for me to be able to do this thesis because many big things in life happened at the same time. Thank you my dear relatives and friends Mikko, Essi, Hertta, Eppu, Sissukka, Esko, Annukka, Hannu, Pia, Jussi, Anne, Esa, Inkku-mummi, Eeva-mummi, Aili-mummi, Riikka, Maria, Maija M., Anna, Artur, Katja, Kaisa T., Lotta, Niina, Aada, Hilla, Marjaana, Maija H., Kaisa R., Nerea, Steve, Jaakko, Mari, Sonja, Maiju, Eini, Ilona, Guille, Linda, Markku, Nauku, Petteri, Spotnik and Anna-Kaisa. Some of you are not here anymore or I see you very rarely, but all of you have supported me so much in your own special ways.

The two most important supporters during this project have been my dearest parents. How can I ever thank you enough? Äiti ja iskä, kuinka voisin kiittää teitä tarpeeksi kaikesta tuesta, mitä olen teiltä saanut? Äiti, olet suurin esikuvani! En tunne ketään toista, joka olisi yhtä sitkeä, epäitsekäs ja ymmärtäväinen kuin sinä. Iskä, sinä olet paras opettajani ja neuvonantajani. Kiitos kun olette aina tukenani, ja antaneet minun samoilla omia metsäpolkujani.

Besides this thesis, I have also given birth to a child. Onni, you are so incredible person, so smart and sensitive, and full of laughter and joy. I have learned so much from you, and I am so grateful to be your mother. I love you forever. Thank you Ossi for sharing the parenthood and taking care of Onni when I was doing the field work for very long days for months, or going to scientific meetings etc. Thank you also for tolerating the usage of the sauna as a huge dryer for the fungal samples for several months in a row.

Jouni, my bear, I love you so much! It is hard to find the words, again. Maybe starting a relationship with a woman finalising her PhD was not that great idea, but if you ask me, and my thesis opinion, we are very happy that you appeared into our lives at the most critical moment. Thank you for helping me to find my piece of mind and taking me to your cottage on the amazing island in the Southern Konnevesi National Park. Many of the chapters of this thesis were born there in the hammock, admiring the most natural boreal nature. Thank you so much for your interest towards my work, your helpful comments, your patience when I have forced you to listen my presentations, and most of all, thank you so much for your love.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Lahopuu ja sienet: havaitseminen, monimuotoisuus ja suojelu boreaalisissa metsissä

Ihminen uhkaa ja köyhdyttää toimillaan luonnon monimuotoisuutta jatkuvasti kiihtyvällä nopeudella. Jotta voisimme onnistuneesti suojella luonnon monimuotoisuutta, tulisi meillä ensin olla kattava ymmärrys erilaisten tekijöiden vaikutuksista eliöiden selviytymiseen ja levinneisyyteen. Yksilö- ja populaatiobiologisen tiedon lisäksi tarvitsemme tietoa etenkin yhteisöistä, jolloin myös lajien väliset moninaiset vuorovaikutukset on mahdollista ottaa huomioon. Tietyssä paikassa, tiettynä aikana elävää lajiryhmää kutsutaan yhteisöksi. Erilaiset teoriat, joilla on aikojen saatossa pyritty selittämään yhteisöjen monimuotoisuutta, liittyvät perimmäisesti neljän pääprosessin tai niiden yhdistelmien alle. Näitä ovat valinta, lajiutuminen, ajautuminen ja leviäminen.

Metsätalouden toimien seurauksena metsien puuston ja lahopuuston rakenne on yksinkertaistunut ja nuorentunut, ja lahopuun määrä on huomattavasti vähentänyt. Lisäksi metsien pirstoutuminen on vaikuttanut metsien jatkuvuuteen, eli siihen kuinka kauan sopiva elinympäristö metsässä on saatavilla. Muun muassa näiden muutosten seurauksena etenkin lahopuulla elävä lajisto on uhanalaistunut voimakkaasti. Lahopuiden sienet ovat merkittävä osa lahopuiden lajiyhteisöä ja muodostavat toiminnallisesti hyvin tärkeän ja monimuotoisen eliöryhmän. Ne ovat päävastuussa puuaineksen lahottamisesta ja ovat siten tärkeitä ravinteiden ja hiilen kierrättämisessä takaisin luonnon kiertokulkuun.

Perinteisesti lahopuulla eläviä sieniä tutkittaessa on huomioitu vain suhteellisen helposti havaittavat lajit, kuten isokokoisia ja pitkäikäisiä itiöemiä tuottavat kääväkkäät. Näiden lajien yhteisöekologia ja luonnonsuojelubiologia tunnetaan jo suhteellisen hyvin Pohjois-Euroopassa. Suurin osa lahopuun sienilajeista on kuitenkin pieniä ja huomaamattomia itiöemiä tuottavia lajeja, joista monet ovat ekologisesti ja taksonomisesti huonosti tunnettuja. Myös metsien lahopuuston tutkimuksissa on juuri pienikokoinen lahopuu jätetty vähemmälle huomiolle.

Väitöskirjassani tutkin miten erilaiset lahopuiden sienilajit ja lahopuukappaleet ovat havaittavissa, sekä minkälainen yhteys metsän ja kasvualustan laadulla on lahopuun sieniyhteisöjen monimuotoisuuteen. Aineistot kerättiin siten, että kaikki pienimmätkin silmin havaittavat kohdesieniryhmät kartoitettiin tutkituilta lahopuilta. Tarkan kartoituksen ansiosta saatiin uutta tietoa erityisesti monista huomaamattomista kotelosienistä, orvakoista ja hyytelösienistä.

Sienten itiöemätuotannon fenologialla, eli itiöemien tuotannon ajankohdalla ja kestolla, voi olla suuri vaikutus sienilajien havaittavuuteen. Näitä biologisestikin tärkeitä ominaisuuksia koskevat tutkimukset ovat kuitenkin yllättävän harvinaisia. Seurasin erittäin tarkasti koivun ja männyn lahopuulla elävien sienten itiöemätuotantoa yhden kasvukauden aikana yhdessä luonnonti-

laisenkaltaisessa metsässä. Sieniryhmät, joilla oli erilaiset itiöemämorfologiat, erosivat merkitsevästi toisistaan itiöemätuotannon fenologian suhteen. Ero johtui pääosin siitä, että helttasienimäiset sienet tuottivat itiöemiä lyhyemmän aikaa kuin muut ryhmät.

Metsän lahopuuprofiili, missä metsän lahopuun määrä on jaettu luokkiin halkaisijan ja lahoasteen suhteen, on hyödyllinen työväline metsän ominaisuuksien ja häiriöhistorian kuvaamisessa. Kuitenkin sellaiset lahopuuprofiilit, joissa on mukana niin suuri kuin pienikin lahopuu ovat harvinaisia. Myöskään kartoitusmenetelmien vaikutusta lahopuun määrän arvioihin ei ole usein testattu. Arvioin yhden luonnontilaisen kaltaisen metsän eri puulajien lahopuukappaleiden lukumäärät koko metsässä ja tilavuudet hehtaarilla. Sain selville, että pienikokoisten lahopuukappaleiden määrä oli valtava, mutta määrä väheni merkittävästi, kun kappaleen halkaisija kasvoi alle senttimetristä 2-3:n senttimetriin. Puulajien runsaus-halkaisija jakaumat erosivat kuitenkin selvästi toisistaan. Esimerkiksi kuusilahopuu koostui lukumääräisesti pääasiassa pienimmistä kappaleista, kun taas haapalahopuusta suurempi osuus oli suurempia kappaleita. Vertaillakseni eri puulajien esiintymistä metsässä muodostin tilavuuteen perustuvan lahopuuprofiilin metsän valtapuulajeille, koivulle, haavalle, männylle ja kuuselle. Suurin osa metsän lahopuusta oli tilavuudessa mitattuna koivua (62 %) ja suurikokoista (< 10 cm halkaisijaltaan). Havaitsin myös, että luotettavaan lahopuukappaleiden lukumäärän arvioon vaadittava tutkimusalojen (10 m x 10 m) määrä riippui puulajista. Määrään vaikuttaa muun muassa puulajin kasvutapa. Esimerkiksi yleisellä ja tasaisesti maisemassa kasvavalla kuusella tarvittiin noin 20 tutkimusalaa, kun taas haavalla, joka kasvaa ryhmissä kasvullisesta lisääntymistavastaan johtuen, ja joka on muutenkin kuusta harvalukuisempi, tarvittiin noin 50 tutkimusalaa. Mikäli tavoitteena olisi arvioida metsän lahopuukappaleiden kokonaismäärää, jo kymmenen satunnaisesti sijoitettua tutkimusalaa antaa riittävän luotettavan arvion.

Tutkin metsän ja lahopuun jatkuvuuden vaikutusta sieniyhteisöihin pystyyn kuolleilla männyillä ja metsän luonnontilaisuuden vaikutusta koivun, kuusen, männyn ja haavan suurikokoisilla maapuilla eläviin sieniyhteisöihin. Kartoitin kaikki seksuaalisia itiöemiä tekevät jäkälöitymättömät sienet ja *Micarea*-suvun jäkälät (vain pystyyn kuolleilta männyiltä) tutkimusrungoilta kussakin 14 luonnontilaisen kaltaisessa metsässä. Metsän jatkuvuudella ei ollut yhteyttä pystyyn kuolleiden mäntyjen sienten lajirikkauteen, mutta *Micarea*-jäkälien lajirikkaus kasvoi mitä pidempi aika oli kulunut tutkimusmännyn kuolemasta. Maapuiden sieniyhteisöjen kokonaislajirikkauden ja metsän luonnontilaisuuden välillä oli merkitsevä, mutta heikko positiivinen yhteys, niin kohde- kuin tutkimusrunkotasolla. Kohdetasolla yhteys johtui mäntyjen kotelosienten korkeammasta lajirikkaudesta metsän luonnontilaisuuden kasvaessa, kun taas runkotasolla yhteys johtui lakillisen muotoryhmän suuremmasta lajirikkaudesta kuusella. Useimmilla muotoryhmillä ei ollut merkitsevää vastetta luonnontilaisuuteen, viitaten siihen, että aiemmin käsitellyssä olleet, mutta nyt suojellut metsät ovat jo hyviä suojelualueita suurimmalle osalle sieniryhmistä. Lahopuun laji selitti eniten sieniyhteisöjen koostumusta, kun taas muotoryhmien koostu-

musta tietyllä puulajilla eniten selittävät tekijät riippuivat ryhmästä ja kyseessä olevasta puulajista.

Puulajin tiedetään olevan yksi tärkeimmistä lahopuiden sieniyhteisöjen koostumuksen määrittäjistä. Kuitenkaan puulajin vaikutusta sienten itiöemä- ja itiömorfologiaan ei tunneta. Yleisesti ottaen havaitsin, että lehtipuilla sieniyhteisöt olivat lajirikkaampia kuin havupuilla, ja että erityisesti maljamaiset ja pullomaiset itiöemäryhmät olivat erikoistuneet elämään lehtipuilla. Pinnanmyötäiset ja lakilliset ryhmät olivat taas erikoistuneet havupuiden lahopuuhun. Lehtilahopuilla elävillä sienillä oli keskimäärin suuremmat ja pitkulaisemmat itiöt, kun taas havupuilla ne olivat keskimäärin pienemmät ja pallomaisemmat. Yhteisöjen keskimääräinen itiökoko myös kasvoi lahopuun koon kasvaessa.

Väitöskirjani tulokset osoittavat, että lahopuiden ja niiden sienten kartoituksia suunniteltaessa täytyy ottaa huomioon, mitä puulajia ja sieniryhmää on tarkoitus tutkia. Sieniryhmät myös reagoivat eritavoin metsän käsittelyhistoriaan, ja tietyn ryhmän vaste voi vielä vaihdella puulajista riippuen. Tästä johtuen lahopuiden sienten suojelun suunnittelun ja toteutuksen tulisi olla vähintään ryhmäkohtaista. Puun laadun vaikutus näkyy sieniyhteisöjen lajikoostumuksen lisäksi lajien itiöemien ja itiöiden morfologiassa. Tulosteni perusteella voidaan arvioida, mihin lajeihin tai lajiryhmiin erilaisilla metsänkäsittelyn toimilla on negatiivinen tai positiivinen vaikutus.

REFERENCES

Aakala T. 2010. Coarse woody debris in late-successional Picea abies forests in northern Europe: Variability in quantities and models of decay class dynamics. *For. Ecol. Manage.* 260: 770–779.

Aakala T., Kuuluvainen T., Wallenius T. & Kauhanen H. 2011. Tree mortality episodes in the intact Picea abies-dominated taiga in the Arkhangelsk region of northern European Russia. *J. Veg. Sci.* 22: 322–333.

Abadie J.C., Machon N., Muratet A. & Porcher E. 2011. Landscape disturbance causes small-scale functional homogenization, but limited taxonomic homogenization, in plant communities. *J. Ecol.* 99: 1134–1142.

Abrego N., Bässler C., Christensen M. & Heilmann-Clausen J. 2015. Implications of reserve size and forest connectivity for the conservation of wood-inhabiting fungi in Europe. *Biol. Conserv.* 191: 469–477.

Abrego N., García-Baquero G., Halme P., Ovaskainen O. & Salcedo I. 2014. Community turnover of wood-inhabiting fungi across hierarchical spatial scales. *PLoS One* 9: e103416.

Abrego N., Halme P., Purhonen J. & Ovaskainen O. 2016. Fruit body based inventories in wood-inhabiting fungi: Should we replicate in space or time? *Fungal Ecol.* 20: 225–232.

Abrego N., Norberg A. & Ovaskainen O. 2017. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. *J. Ecol.*: https://doi.org/10.1111/1365-2745.12722.

Abrego N. & Salcedo I. 2011. How does fungal diversity change based on woody debris type? A case study in Northern Spain. *Ekologija* 57: 109–119.

Abrego N. & Salcedo I. 2013. Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality? *For. Ecol. Manage.* 291: 377–385.

Abrego N. & Salcedo I. 2014. Response of wood-inhabiting fungal community to fragmentation in a beech forest landscape. *Fungal Ecol.* 8: 18–27.

Agren J. & Zackrisson O. 1990. Age and size structure of Pinus sylvestris populations on mires in Central and Northern Sweden. *J. Ecol.* 78: 1049–1062.

Aguilar-Trigueros C.A., Hempel S., Powell J.R., Anderson I.C., Antonovics J., Bergmann J., Cavagnaro T.R., Chen B., Hart M.M., Klironomos J., Petermann J.S., Verbruggen E., Veresoglou S.D. & Rillig M.C. 2015. Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biol. Rev.* 29: 34–41.

Ahti T., Hämet-Ahti L. & Jalas J. 1968. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* 5: 169–211.

Angelstam P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sci.* 9: 593–602.

Angelstam P.K., Boutin S., Schmiegelow F., Villard M., Drapeau P., Host G., Innes J., Isachenko G., Kuuluvainen T., Mönkkönen M., Niemelä J., Niemi G., Roberge J., Spence J. & Stone D. 2004. Targets for boreal forest biodiversity conservation – a rationale for macroecological research and adaptive management. *Ecol. Bull.* 51: 487–509.

Anonymous. 1993. Convention on biological diversity (with annexes). Concluded at Rio de Janeiro on 5 June 1992. *United Nations – Treaty Ser.* 1760: 142–382.

Arnstadt T., Hoppe B., Kahl T., Kellner H., Krüger D., Bauhus J. & Hofrichter M. 2016. Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of Fagus sylvatica, Picea abies and Pinus sylvestris. *For. Ecol. Manage.* 382: 129–142.

Arrhenius O. 1921. Species and Area. *J. Ecol.* 9: 95–99.

Ausmus B.S. 1977. Regulation of wood decomposition rates by Arthropod and Annelid populations. *Ecol. Bull.* 25: 180–192.

Baber K., Otto P., Kahl T., Gossner M.M., Wirth C., Gminder A. & Bässler C. 2016. Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi. *For. Ecol. Manage.* 377: 161–169.

Bader P., Jansson S. & Jonsson B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biol. Conserv.* 72: 355–362.

Bailey L.L., Simons T.R. & Pollock K.H. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecol. Appl.* 14: 692–702.

Bässler C., Ernst R., Cadotte M., Heibl C. & Müller J. 2014. Near-to-nature logging influences fungal community assembly processes in a temperate forest. *J. Appl. Ecol.* 51: 939–948.

Bässler C., Müller J., Cadotte M.W., Heibl C., Bradtka J.H., Thorn S., Halbwachs H., Forest B., Park N. & Str F. 2016. Functional response of lignicolous fungal guilds to bark beetle deforestation. *Ecol. Indic.* 65: 149–160.

Bates D., Maechler M., Bolker B.M., Walker S., Christensen R.H.B., Singmann H., Dai B., Grothendieck G. & Green P. 2016. lme4: Linear Mixed-Effects Model using 'Eigen' and S4, version 1.1-12. *https://cran.r-project.org/web/packages/lme4/lme4*: 31.12.2016.

Berglund H., Edman M. & Ericson L. 2005. Temporal variation of wood-fungi diversity in boreal old-growth forests: Implications for monitoring. *Ecol. Appl.* 15: 970–982.

Boddy L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarce woody debris. *Ecol. Bull.* 49: 43–56.

Boddy L. & Jones T.H. 2008. Interactions between Basidiomycota and invertebrates. In: Boddy L., Frankland J.C. & West P. van (eds.), *Ecology of Saprotrophic Basidiomycetes*, Elsevier, London, pp. 155–179.

Boer W. de & Val A. van der. 2008. Interactions between saprotrophic basidiomycetes and bacteria. In: Boddy L., Frankland J.C. & West P. van (eds.), *Ecology of saprotrophic basidiomycetes*, Elsevier, London, pp. 141–151.

von Bonsdorff T., Haikonen V., Huhtinen S., Härkönen M., Kaukonen M., Kirsi M., Kosonen L., Kytövuori I., Ohenoja E., Paalamo P., Salo P., Sivonen E., Vauras J., Kotiranta H., Junninen K., Saarenoksa R. & Kinnunen J. 2010. Sienet. In: Rassi P., Hyvärinen E., Juslén A. & Mannerkoski I. (eds.), *Suomen lajien uhanalaisuus - Punainen kirja*, Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, pp. 231–277.

von Bonsdorff T., Niskanen T., Liimatainen K., Kytövuori I., Huhtinen S., Vauras J., Höijer P., Kekki T., Lahti M., Puolasmaa A., Purhonen J., Halme P., Jakobsson S., Toivonen M. & Söderholm U. 2016. New national and regional biological records for Finland 8. Contributions to agaricoid, gastroid and ascomycetoid taxa of fungi 5. *Memo. Soc. pro Fauna Flora Fenn.* 92: 120–128.

von Bonsdorff T., Niskanen T., Liimatainen K., Kytövuori I., Vauras J., Huhtinen S., Höijer P., Kekki T., Kosonen T., Tervonen K., Purhonen J., Halme P., Pennanen M. & Marsh T. 2015. New national and regional biological records for Finland 5. Contributions to agaricoid and ascomycetoid taxa of fungi 4. *Memo. Soc. pro Fauna Flora Fenn.* 91: 56–66.

Brūmelis G., Jonsson B.G., Kouki J., Kuuluvainen T. & Shorohova E. 2011. Forest naturalness in Northern Europe: Perspectives on processes, structures and species diversity. *Silva Fenn.* 45: 807–821.

Cajander A.K. 1949. Forest types and their significance. *Acta For. Fenn.* 56: 1–69.

Calhim S., Halme P., Petersen J.H., Læssøe T., Bässler C. & Heilmann-Clausen J. 2018. Fungal spore diversity reflects substrate-specific deposition challenges. *Sci. Rep.* 8: 1–9.

Chase J.M. & Myers J.A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philos. Trans. R. Soc. B Biol. Sci.* 366: 2351–2363.

Clavel J., Julliard R. & Devictor V. 2011. Worldwide decline of specialist species : toward a global functional homogenization? *Front. Ecol. Environ.* 9: 222–228.

Coppins B.J. 1983. A taxonomic study of the lichen genus Micarea in Europe. *Bull. Br. Museum Nat. Hist. Bot.* 11: 1–204.

Czarnota P. 2007. The lichen genus Micarea (Iecanorales, Ascomycota) in Poland. *Polish Bot. Stud.* 23: 1–197.

Czarnota P. & Guzow-Krzemínska B. 2010. A phylogenetic study of the Micarea prasina group shows that Micarea micrococca includes three distinct lineages. *Lichenologist* 42: 7–21.

Dawson S.K., Boddy L., Halbwachs H., Bässler C., Crowther T.W., Heilmann-Clausen J., Nordén J., Ovaskainen O. & Jönsson M. 2018. Handbook for standardised measurement of macrofungal functional traits; a start with basidiomycete wood fungi. *Funct. Ecol.*: doi: 10.1111/1365-2435.13239.

Devictor V., Julliard R., Couvet D., Lee A. & Jiguet F. 2007. Functional homogenization effect of urbanization on bird communities. *Conserv. Biol.* 21: 741–751.

Dickie I. a., Kałucka I., Stasińska M. & Oleksyn J. 2010. Plant host drives fungal phenology. *Fungal Ecol.* 3: 311–315.

Dowding P. 1981. Nutrient uptake and allocation during substrate exploitation by fungi. In: Wicklow D.T. & Carroll G.C. (eds.), *The Fungal Community. Its Organization and Role in the Ecosystems*, Marcel Dekker Inc, New York, pp. 612–636.

Edenius L., Ericsson G., Kempe G., Bergström R. & Danell K. 2011. The effects of changing land use and browsing on aspen abundance and regeneration: A 50-year perspective from Sweden. *J. Appl. Ecol.* 48: 301–309.

Edman M. & Jonsson B.G. 2001. Spatial pattern of downed logs and wood-living fungi in an old-growth spruce forest. *J. Veg. Sci.* 12: 609–620.

Eräjää S., Halme P., Kotiaho J.S., Markkanen A. & Toivanen T. 2010. The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. *Silva Fenn.* 44: 203–211.

Esseen P.A., Ehnström B., Ericson L. & Sjöberg K. 1997. Boreal forests. *Ecol. Bull.* 46: 16–47.

Field S.A., O'Connor P.J., Tyre A.J. & Possingham H.P. 2007. Making monitoring meaningful. *Austral Ecol.* 32: 485–491.

Field S., Tyre A. & Possingham H. 2005. Optimizing Allocation of Monitoring Effort Under Economic and Observational Constraints. *J. Wildl. Manage.* 69: 473–482.

Franklin J.F., Shugart H.H. & Harmon M.E. 1987. Tree Death as an Ecological Process. *Bioscience* 37: 550–556.

Frelich L.E. 2002. *Forest Dynamics and Disturbance Regimes: studies from temperate evergreen-temperate forests*. Cambridge University Press, Cambridge.

Fritts H.C. & Swetnam T.W. 1989. Relationships among beech bark disease, climate, radial growth response and mortality of American beech in northern Maine, USA. *Adv. Ecol. Res.* 19: 111–188.

Fritz Ö., Gustafsson L. & Larsson K. 2008. Does forest continuity matter in conservation? - A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biol. Conserv.* 141: 655–668.

Gange a C., Gange E.G., Sparks T.H. & Boddy L. 2007. Rapid and recent changes in fungal fruiting patterns. *Science (80-.).* 316: 71.

Garrard G.E., Bekessy S. a., McCarthy M. a. & Wintle B. a. 2008. When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecol.* 33: 986–998.

Grinnell J. 1922. The role of the 'accidental'. *Auk* 39: 373–380.

Groven R., Rolstad J., Storaunet K.O. & Rolstad E. 2002. Using forest stand recostructions to assess the role of structural continuity for late successional species. *For. Ecol. Manage.* 164: 39–55.

Halme P. & Kotiaho J.S. 2012. The importance of timing and number of surveys in fungal biodiversity research. *Biodivers. Conserv.* 21: 205–219.

Halme P., Marjakangas E.-L., Purhonen J., Juutilainen K., Huhtinen S., Kotiranta H., Kotiaho J.S. & Abrego N. 2018. The species richness and population sizes of wood-inhabiting fungi in an especially thoroughlt studied forest - implications for fungal conservation. *prep*.

Halme P., Ódor P., Christensen M., Piltaver A., Veerkamp M., Walleyn R., Siller I. & Heilmann-Clausen J. 2013. The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. *Biol. Conserv.* 168: 24–30.

Heilmann-Clausen J. & Christensen M. 2004. Does size matter? *For. Ecol. Manage.* 201: 105–117.

Heilmann-Clausen J. & Christensen M. 2005. Wood-inhabiting macrofungi in Danish beech-forests ? conflicting diversity patterns and their implications in a conservation perspective. *Biol. Conserv.* 122: 633–642.

Hibbett D.S., Binder M., Bischoff J.F., Blackwell M., Cannon P.F., Eriksson O.E., Huhndorf S., James T., Kirk P.M., Lücking R., Thorsten Lumbsch H., Lutzoni F., Matheny P.B., McLaughlin D.J., Powell M.J., Redhead S., Schoch C.L., Spatafora J.W., Stalpers J. a, Vilgalys R., Aime M.C., Aptroot A., Bauer R., Begerow D., Benny G.L., Castlebury L. a, Crous P.W., Dai Y.-C., Gams W., Geiser D.M., Griffith G.W., Gueidan C., Hawksworth D.L., Hestmark G., Hosaka K., Humber R. a, Hyde K.D., Ironside J.E., Kõljalg U., Kurtzman C.P., Larsson K.-H., Lichtwardt R., Longcore J., Miadlikowska J., Miller A., Moncalvo J.-M., Mozley-Standridge S., Oberwinkler F., Parmasto E., Reeb V., Rogers J.D., Roux C., Ryvarden L., Sampaio J.P., Schüssler A., Sugiyama J., Thorn R.G., Tibell L., Untereiner W. a, Walker C., Wang Z., Weir A., Weiss M., White M.M., Winka K., Yao Y.-J. & Zhang N. 2007. A higher-level phylogenetic classification of the Fungi. *Mycol. Res.* 111: 509–547.

Hofgaard a. 1993. 50 years of change in a Swedish boreal old-growth Picea abies forest. *J. Veg. Sci.* 4: 773–782.

Holmes R.L. 1983. Computer-assisted quality control in tree- ring dating and measurement. *Tree-ring Bull.* 43: 69–78.

Hoppe B., Purahong W., Wubet T., Kahl T., Bauhus J., Arnstadt T., Hofrichter M., Buscot F. & Krüger D. 2016. Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Divers.* 77: 367–379.

Hussein T., Norros V., Hakala J., Petäjä T., Aalto P.P., Rannik Ü., Vesala T. & Ovaskainen O. 2013. Species traits and inertial deposition of fungal spores. *J. Aerosol Sci.* 61: 81–98.

Järvinen O. & Väisänen R.A. 1975. Estimating relative densities of breeding birds by the line transect method. *Oikos* 26: 316–322.

Johansson P., Rydin H. & Thor G. 2007. Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. *Ecoscience* 14: 81–91.

Jonsson B.G., Ekström M., Esseen P.A., Grafström A., Ståhl G. & Westerlund B. 2016. Dead wood availability in managed Swedish forests - Policy outcomes and implications for biodiversity. *For. Ecol. Manage.* 376: 174–182.

Jonsson B.G., Kruys N. & Ranius T. 2005. Ecology of Species Living on Dead Wood – Lessons for Dead Wood Management. *Silva Fenn.* 39: 289–309.

Jönsson M. & Jonsson B.G. 2007. Assessing coarse woody debris in Swedish woodland key habitats: Implications for conservation and management. *For. Ecol. Manage.* 242: 363–373.

Jönsson M., Ruete A., Kellner O., Gunnarsson U. & Snäll T. 2016. Will forest conservation areas protect functionally important diversity of fungi and lichens over time? *Biodivers. Conserv.*: DOI 10.1007/s10531-015-1035-0.

Junninen K. & Komonen A. 2011. Conservation ecology of boreal polypores: A review. *Biol. Conserv.* 144: 11–20.

Junninen K., Similä M., Kouki J. & Kotiranta H. 2006. Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. *Ecography (Cop.).* 29: 75–83.

Juutilainen K., Halme P., Kotiranta H. & Mönkkönen M. 2011. Size matters in studies of dead wood and wood-inhabiting fungi. *Fungal Ecol.* 4: 342–349.

Juutilainen K., Mönkkönen M., Kotiranta H. & Halme P. 2017. Resource use of wood-inhabiting fungi in different boreal forest types. *Fungal Ecol.* 27: 96–106.

Kahl T., Arnstadt T., Baber K., Bässler C., Bauhus J., Borken W., Buscot F., Floren A., Heibl C., Hessenmöller D., Hofrichter M., Hoppe B., Kellner H., Krüger D., Linsenmair K.E., Matzner E., Otto P., Purahong W., Seilwinder C., Schulze E.D., Wende B., Weisser W.W. & Gossner M.M. 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *For. Ecol. Manage.* 391: 86–95.

Kauserud H., Heegaard E., Büntgen U., Halvorsen R., Egli S. & Senn-irlet B. 2012. Warming-induced shift in European mushroom fruiting phenology. *PNAS* 109: 14488–14493.

Kazartsev I., Shorohova E., Kapitsa E. & Kushnevskaya H. 2018. Decaying Picea abies log bark hosts diverse fungal communities. *Fungal Ecol.* 33: 1–12.

Kéry M., Spillmann J.H., Truong C. & Holderegger R. 2006. How biased are estimates of extinction probability in revisitation studies? *J. Ecol.* 94: 980–986.

Komonen A. 2003. Hotspots of insects diversity in boreal forests. *Conserv. Biol.* 17: 976–981.

Komonen A. 2005. Local spatial pattern in the occurrence of two congeneric wood-decaying fungi in an old-growth boreal forest. *Scand. J. For. Res.* 20: 393–399.

Komonen A. & Müller J. 2018. Dispersal ecology of deadwood organisms and connectivity conservation. *Conserv. Biol.* 32: 535–545.

Komonen A., Schroeder L.M. & Weslien J. 2011. Ips typographus population development after a severe storm in a nature reserve in southern Sweden. *J. Appl. Entomol.* 135: 132–141.

Kotiranta H., Saarenoksa R. & Kytövuori I. 2009. Aphyllophoroid fungi of Finland. A check-list with ecology, distribution, and threat categories. *Norrlinia* 19: 1–223.

Kouki J., Arnold K. & Martikainen P. 2004. Long-term persistence of aspen - A key host for many threatened species - Is endangered in old-growth conservation areas in Finland. *J. Nat. Conserv.* 12: 41–52.

Kouki J., Löfman S., Martikainen P., Rouvinen S. & Uotila A. 2001. Forest Fragmentation in Fennoscandia: Linking Habitat Requirements of Wood-associated Threatened Species to Landscape and Habitat Changes. *Scand. J. For. Res.* 16: 27–37.

Krah F.S., Seibold S., Brandl R., Baldrian P., Müller J. & Bässler C. 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. *J. Ecol.*: 1–15.

Kubartová A., Ottosson E., Dahlberg A. & Stenlid J. 2012. Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Mol. Ecol.* 21: 4514–4532.

Kuuluvainen T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: The complexity challenge. *Ambio* 38: 309–315.

Kuuluvainen T., Penttinen A., Leinonen K. & Nygren M. 1996. Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: An example from boreal spruce forest in southern Finland. *Silva Fenn.* 30: 315–328.

Lawrey J.D. 1991. Biotic interactions in lichen community development: a review. *Lichenologist* 23: 205–214.

Lindblad I. 1998. Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. *Nord. J. Bot.* 18: 243–255.

Linder P., Elfving B. & Zackrisson O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *For. Ecol. Manage.* 98: 17–33.

Lõhmus A. 2009. Factors of species-specific detectability in conservation assessments of poorly studied taxa: The case of polypore fungi. *Biol. Conserv.* 142: 2792–2796.

Lõhmus A. 2011. Silviculture as a disturbance regime: The effects of clear-cutting, planting and thinning on polypore communities in mixed forests. *J. For. Res.* 16: 194–202.

Lonsdale D., Pautasso M. & Holdenrieder O. 2007. Wood-decaying fungi in the forest: conservation needs and management options. *Eur. J. For. Res.* 127: 1–22.

Lorimer C.G. & Frelich L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.* 19: 651–663.

MacArthur R.H. & Wilson E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton.

Magnusson A., Skaug H.J., Nielsen A., Berg C.W., Kristensen K., Maechler M., Bentham K.J. van, Bolker B.M. & Brooks M.E. 2018. glmmTMB: Generalized Linear Mixed Models using Template Model Builder. *https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf*: 30.08.2018.

McCarthy J. 2001. Erratum: Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environ. Rev.* 9: 129.

McGill B.J., Enquist B.J., Weiher E. & Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21: 178–185.

Molina R., Horton T.R., Trappe J.M. & Marcot B.G. 2011. Addressing uncertainty: How to conserve and manage rare or little-known fungi. *Fungal Ecol.* 4: 134–146.

Moore D., Gange A.C., Gange E.G. & Boddy L. 2008. Fruit bodies: Their production and develpoment in relation to environment. In: Boddy L., Frankland J.C. & West P. van (eds.), *Ecology of Saprotrophic Basidiomycetes*, Elsevier, London, pp. 79–102.

Mouillot D., Graham N.A.J., Villéger S., Mason N.W.H. & Bellwood D.R. 2013. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28: 167–177.

Niemelä J. 2000. Biodiversity monitoring for decision-making. *Ann. Zool. Fennici* 37: 307–317.

Niemelä T. 2005. Käävät, puiden sienet. *Norrlinia* 13: 1–320.

Niemelä T., Wallenius T. & Kotiranta H. 2002. The kelo tree, a vanishing substrate of specified wood-inhabiting fungi. *Polish Bot. J.* 47: 91–101.

Nilsson C., Stjernquist I., Bärring L., Schlyter P., Jönsson A.M. & Samuelsson H. 2004. Recorded storm damage in Swedish forests 1901 – 2000. *For. Ecol. Manage.* 199: 165–173.

Nordén B. & Appelqvist T. 2001. Conceptual problems of ecological continuity and its bioindicators. *Biodivers. Conserv.* 10: 779–791.

Nordén B., Dahlberg A., Brandrud T.E., Fritz Ö., Ejrnaes R. & Ovaskainen O. 2014. Effects of Ecological Continuity on Species Richness and Composition in Forests and Woodlands: A Review. *Ecoscience* 21: 34–45.

Nordén J., Penttilä R., Siitonen J., Tomppo E. & Ovaskainen O. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101: 701–712.

Nordén B., Ryberg M., Götmark F. & Olausson B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biol. Conserv.* 117: 1–10.

Norros V., Karhu E., Nordén J., Vähätalo A. V. & Ovaskainen O. 2015. Spore sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. *Ecol. Evol.* 5: 3312–3326.

Norros V., Penttilä R., Suominen M. & Ovaskainen O. 2012. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. *Oikos* 121: 961–974.

Norros V., Rannik Ü., Hussein T., Petäjä T., Vesala T. & Ovaskainen O. 2014. Do small spores disperse further than large spores? *Ecology* 95: 1612–1621.

Ódor P., Heilmann-Clausen J., Christensen M., Aude E., Dort K.W. van, Piltaver A., Siller I., Veerkamp M.T., Walleyn R., Standovár T., Hees A.F.M. van, Kosec J., Matočec N., Kraigher H. & Grebenc T. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biol. Conserv.* 131: 58–71.

Oksanen J., Blanchet, F. Guillaume Friendly M., Roeland K., Legendre P., McGlinn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens, M. Henry H. Szoecs E. & Wagner H. 2017. vegan: Community Ecology Package. R package version 2.4-4. *https://cran.r-project.org/web/packages/vegan/index.html*: 30.12.2017.

Ottosson E., Kubartova A., Edman M., Jönsson M., Lindhe A., Stenlid J. & Dahlberg A. 2015. Diverse ecological roles within fungal communities in decomposing logs of Picea abies. *FEMS Microbiol. Ecol.* 91: 1–13.

Ovaskainen O., Schigel D., Ali-Kovero H., Auvinen P., Paulin L., Nordén B. & Nordén J. 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. *ISME J.* 7: 1696–1709.

Ovaskainen O., Tikhonov G., Norberg A., Guillaume Blanchet F., Duan L., Dunson D., Roslin T. & Abrego N. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecol. Lett.* 20: 561–576.

Paillet Y., Bergès L., Hjältén J., Ódor P., Avon C., Bernhardt-Römermann M., Bijlsma R.-J., Bruyn L. De, Fuhr M., Grandin U., Kanka R., Lundin L., Luque S., Magura T., Matesanz S., Mészáros I., Sebastià M.-T., Schmidt W., Standovár T., Tóthmérész B., Uotila A., Valladares F., Vellak K. & Virtanen R. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24: 101–112.

Palmer M.W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobot. Phytotaxon.* 29: 511–530.

Peay K.G., Kennedy P.G. & Bruns T.D. 2008. Fungal community ecology: A hybrid beast with a molecular master. *Bioscience* 58: 799–810.

Penttilä R., Siitonen J. & Kuusinen M. 2004. Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. *Biol. Conserv.* 117: 271–283.

Petchey O.L. & Gaston K.J. 2006. Functional diversity: Back to basics and looking forward. *Ecol. Lett.* 9: 741–758.

Preston F.W. 1960. Time and space and the variation of species. *Ecology* 41: 612–627.

Pretzsch H. 2009. *Forest Dynamics, Growth and Yield*. Springer-Verlag Berlin Heidelberg, Freising.

R Core Team. 2015. R: A language and environment for statistical computing.

R Core Team. 2016. R: A language and environment for statistical computing.

R Core Team. 2017. R: A language and environment for statistical computing.

Rajala T., Peltoniemi M., Pennanen T. & Mäkipää R. 2010. Relationship between wood-inhabiting fungi determined by molecular analysis (denaturing gradient gel electrophoresis) and quality of decaying logs. *Can. J. For. Res.* 40: 2384–2397.

Rassi P., Alanen A., Kanerva T. & Mannerkoski I. 2001. *The red list of Finnish species.* Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.

Regent Instruments Inc. 2015. WinDENDRO software for annual tree-ring analysis.

Renvall P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35: 1–51.

Ripple W.J., Wolf C., Newsome T.M., Galetti M., Alamgir M., Crist E., Mahmoud M.I. & Laurance W.F. 2017. World scientists' warning to humanity: A second notice. *Bioscience* 67: 1026–1028.

Rolstad J., Sætersdal M., Gjerde I. & Storaunet K.O. 2004. Wood-decaying fungi in boreal forest: Are species richness and abundances influenced by small-scale spatiotemporal distribution of dead wood? *Biol. Conserv.* 117: 539–555.

Rosenzweig M.L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.

Royal Botanic Gardens Kew, Landcare Research-NZ & Chinese Academy of Science. 2015. Index Fungorum. *www.indexfungorum.org*: 31.12.2015.

Ruokolainen A., Shorohova E., Penttilä R., Kotkova V. & Kushnevskaya H. 2018. A continuum of dead wood with various habitat elements maintains the diversity of wood-inhabiting fungi in an old-growth boreal forest. *Eur. J. For. Res.*: https://doi.org/10.1007/s10342-018-1135-y.

Sandström F., Petersson H., Kruys N. & Ståhl G. 2007. Biomass conversion factors (density and carbon concentration) by decay classes for dead wood of Pinus sylvestris, Picea abies and Betula spp. in boreal forests of Sweden. *For. Ecol. Manage.* 243: 19–27.

Schigel D. 2007. Fleshy fungi of the genera Armillaria, Pleurotus, and Grifola as habitats of Coleopteran. *Karstenia* 47: 37–48.

Schneider C.A., Rasband W.S. & Eliceiri K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9: 671–675.

Shannon C.D. & Weaver W. 1949. *The mathematical theory of communication*. Univeristy of Illimois Press, Urbana.

Shepperd W.D., Bartos D.L. & Mata S.A. 2001. Above- and below-ground effects of aspen clonal regeneration and succession to conifers. *Can. J. For. Res.* 31: 739–745.

Sherwood M.A. 1981. Convergent evolution in discomycetes from bark and wood. *Bot. J. Linn. Soc.* 82: 15–34.

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49: 11–41.

Simberloff D. 2004. Community Ecology : Is It Time to Move On ? *Am. Nat.* 163: 787–799.

Spies T.A., Franklin J.F. & Thomas T.B. 1988. Coarse Woody Debris in Douglas-Fir Forests of Western Oregon and Washington. *Ecology* 69: 1689–1702.

Stenroos S., Ahti T., Lohtander K., Myllys L. & Haikonen V. 2011. *Suomen jäkäläopas*. Kasvimuseo, Luonnontieteelline keskusmuseo LUOMUS, Helsinki.

Stokland J.N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. *Ecol. Bull.* 49: 57–70.

Stokland J.N. 2012a. Evolution of saproxylic organisms. In: Stokland J.N., Siitonen J. & Jonsson B.G. (eds.), *Biodiversity in dead wood*, Cambridge University Press, Cambridge, pp. 218–247.

Stokland J.N. 2012b. Wood decomposition. In: Stokland J.N., Siitonen J. & Jonsson B.G. (eds.), *Biodiversity in dead wood*, Cambridge University Press, Cambridge, pp. 10–28.

Stokland J.N. 2012c. Host-tree associattions. In: Stokland J.N., Siitonen J. & Jonsson B.G. (eds.), *Biodiversity in dead wood*, Cambridge University Press, Cambridge, pp. 82–109.

Stokland J.N. & Larsson K. 2011. Forest Ecology and Management Legacies from natural forest dynamics : Different effects of forest management on wood-inhabiting fungi in pine and spruce forests. *For. Ecol. Manage.* 261: 1707–1721.

Stokland J.N., Siitonen J. & Jonsson B.G. 2012. *Biodiversity on dead wood*. Cambridge University Press, Cambridge.

Straatsma G., Ayer F. & Egli S. 2001. Species richness, abundance, and phenology of fungal fruit bodies over 21 years in a Swiss forest plot. *Mycol. Res.* 105: 515–523.

Stroud J.T., Bush M.R., Ladd M.C., Nowicki R.J., Shantz A.A. & Sweatman J. 2015. Is a community still a community? Reviewing definitions of key terms in community ecology. *Ecol. Evol.* 5: 4757–4765.

Sverdrup-Thygeson A. & Lindenmayer D.B. 2003. Ecological continuity and assumed indicator fungi in boreal forest: The importance of the landscape matrix. *For. Ecol. Manage.* 174: 353–363.

Terradas J. 2005. Forest dynamics: a broad view of the evolution of the topic, including some recent regional contributions. *Investig. Agrar. Sist. y Recur. For.* 14: 525–537.

Tibell L. 1999. Calicioid lichens and fungi. *Nord. Lichen Flora* 1: 20–94.

Tikka P.S. 1954. Haapametsiköiden rakenteesta ja laadusta: I. Rakenne. *Metsäntutkimuslaitoksen Julk.* 44: 1–33.

Tikka P.S. 1955. Haapametsiköiden rakenteesta ja laadusta: II. Laatu. *Metsäntutkimuslaitoksen Julk.* 45: 1–54.

Tikkanen O.-P., Martikainen P., Hyvärinen E., Junninen K. & Kouki J. 2006. Red-listed boreal forest species of Finland: associations with forst structure, tree species, and decaying wood. *Ann. Zool. Fennici* 43: 373–383.

Tikkanen O.P., Predtechenskaya O., Ruokolainen A. & Heikkilä R. 2017. Recovery of functional groups of fungi and wood-decaying species of conservation concern after variable intensity forest utilization. *Eur. J. For. Res.* 136: 827–837.

Townsend C.R., Begon M. & Harper J.L. 2003. *Essentials of Ecology*. Blackwell Science Ltd, Malden.

Tyre A.J., Tenhumberg B., Field S.A., Niejalke D. & Possingham H.P. 2003. Improving Precision and Reducing Bias in Biological Surveys : Estimating False-Negative Error Rates. *Ecol. Appl.* 13: 1790–1801.

Uliczka H. & Angelstam P. 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography (Cop.)*. 22: 396–405.

Vandermeer J.H. 1972. Niche Theory. *Annu. Rev. Ecol. Syst.* 3: 107–132.

Vellend M. 2010. Conceptual synthesis in community ecology. *Q. Rev. Biol.* 85: 183–206.

Vellend M. 2016. *The theory of ecological communities*. Princeton University Press, New Jersey.

Vellend M., Srivastava D.S., Anderson K.M., Brown C.D., Jankowski J.E., Kleynhans E.J., Kraft N.J.B., Letaw A.D., Macdonald A.A.M., Maclean J.E., Myers-Smith I.H., Norris A.R. & Xue X. 2014. Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos* 123: 1420–1430.

Vergnon R., Dulvy N.K. & Freckleton R.P. 2009. Niches versus neutrality: Uncovering the drivers of diversity in a species-rich community. *Ecol. Lett.* 12: 1079–1090.

Violi H. a., Barrientos-Priego A.F., Wright S.F., Escamilla-Prado E., Morton J.B., Menge J. a. & Lovatt C.J. 2008. Disturbance changes arbuscular mycorrhizal fungal phenology and soil glomalin concentrations but not fungal spore composition in montane rainforests in Veracruz and Chiapas, Mexico. *For. Ecol. Manage.* 254: 276–290.

White E.P., Adler P.B., Lauenroth W.K., Gill R.A., Greenberg D., Kaufman D.M., Rassweiler A., Rusak J.A., Smith M.D., Steinbeck J.R., Waide R.B. & Yao J. 2006. A comparison of the species time relationship across ecosystems and taxonomic groups. *Oikos* 112: 185–195.

Wright D.H. 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41: 496–506.

Yamaguchi D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* 21: 414–416.

ORIGINAL PAPERS

I

DETAILED INFORMATION ON FRUITING PHENOLOGY PROVIDES NEW INSIGHTS ON WOOD-INHABITING FUNGAL DETECTION

by

Purhonen Jenna, Huhtinen Seppo, Kotiranta Heikki, Kotiaho Janne S. & Halme Panu 2016

Fungal Ecology 27:175-177.

Fungal Ecology 27 (2017) 175–177

Contents lists available at ScienceDirect

Fungal Ecology

journal homepage: www.elsevier.com/locate/funeco

Detailed information on fruiting phenology provides new insights on wood-inhabiting fungal detection

Jenna Purhonen [a, *], Seppo Huhtinen [b], Heikki Kotiranta [c], Janne S. Kotiaho [a], Panu Halme [a, d]

[a] Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014, Finland
[b] Herbarium, University of Turku, FI-20014 Turku, Finland
[c] Biodiversity Unit, Finnish Environment Institute, P.O. Box 140, FI-00251, Helsinki, Finland
[d] Jyväskylä University Museum, University of Jyväskylä, P.O. Box 35, FI-40014, Finland

ARTICLE INFO

Article history:
Received 31 January 2016
Received in revised form
15 June 2016
Accepted 30 June 2016
Available online 28 November 2016

Corresponding Editor: Jacob Heilmann-Clausen

Keywords:
Agarics
Ascomycetes
Corticioids
Detectability
Fruit body survey
Fungal conservation
Longevity
Phenology
Polypores
Red-list

ABSTRACT

Fruiting phenology traits may have a large effect on the detection of fungal species. Detailed studies considering these biologically important traits are, however, surprisingly scarce. We conducted a rigorous fruit body monitoring of wood-inhabiting fungal occurrences over one fruiting season. Taxon-specific longevity of the fruiting was different between different morphological groups. This was mainly due to agaric fruiting being shorter than other groups. Different number and timing of surveys are needed to detect the majority of the fruiting taxa of different wood-inhabiting fungal groups.

1. Introduction

Fruit body survey is the most common method used for detecting fungal species occurrences in ecological and conservation research and for national threat assessments (Dahlberg and Mueller, 2011; Halme et al., 2012). However, there is high within and between species variation in the fruiting phenology, i.e. timing and longevity of fruit body production (Berglund et al., 2005; Moore et al., 2008; Dickie et al., 2010; Halme and Kotiaho, 2012). This variation causes a problem of false-negatives, because surveys fail to record all species that are present within the sampling unit. Imperfect detection in turn causes misleading conclusions of species roles in fungal communities and biased population assessments that result in overestimation of extinction probabilities and, therefore, biased assessments of the species' conservation statuses (Kéry et al., 2006; Halme and Kotiaho, 2012; Ovaskainen et al., 2013).

More knowledge of species specific fruiting phenologies would thus be important to improve fungal survey methods. However, only a few studies have investigated in detail how different traits of fruiting may affect the detection of different fungal species (e.g. Lõhmus, 2009; van der Linde et al., 2012). Moreover, all of them have focused on charismatic species such as polypores or agarics.

Hence, here we studied the timing (the starting point for fruit body production) and longevity (length of time during which the fruit bodies are produced and maintained) of fruit body production

* Corresponding author.
E-mail address: jenna.purhonen@jyu.fi (J. Purhonen).

http://dx.doi.org/10.1016/j.funeco.2016.06.007
1754-5048/

of nearly all sexually reproducing groups of wood-inhabiting fungi.

2. Materials and methods

The study site was a 108 ha *Picea abies* dominated forest in southern boreal vegetation zone in Central Finland, set aside from human use around 1860 and protected in 1980s. Decaying trunks of 13 *Betula* sp. and 13 *Pinus sylvestris* were selected with the following criteria: moss coverage and decay stage (Renvall, 1995) of the trunk had to be less than 50% and 5, respectively. The trunks are a subset of a long-term project (see Halme and Kotiaho, 2012).

For each trunk, all sexual fruit body or fruit body group occurrences of wood-inhabiting fungal species visible to the naked eye, excluding lichenized species, were rigorously monitored from mid-May to mid-October with 12 repeated surveys covering the whole snowless season (140 d) of the year 2010 (Appendix 1). See Fig. 5 in Halme et al. (2013) for the approximate trunk surface temperature, light condition and humidity along the study period, measured in close vicinity of the study trunks.

For most occurrences, we were not able to identify the species in the field and specimens were collected for later microscopic identification. The taxa were divided into seven morphological groups based on the form of the fruit bodies; perennial polypores (PolP), annual polypores (PolA), corticioids (Cort), discomycetes (Disc), pyrenomycetes (Pyr), agarics (Agar) and jelly fungi (Jelly). The species nomenclature is based on Index Fungorum (Royal Botanic Gardens Kew et al., 2015).

All fruit bodies belonging to a certain taxon within a trunk were regarded as one occurrence. We considered the first detection (no matter what was the state of the fruiting) of an occurrence as the starting point of its fruiting. The longevity for each occurrence was calculated so that for being present in a specific survey the occurrence was given the longevity of 10 d, except if present in May and June the occurrence was given 20 d for May. The total longevity of an occurrence was then the sum of the days it attained during the whole study period. From these occurrence-specific longevities we calculated the taxon-specific mean and standard deviation of fruiting longevity for all of the detected taxa over all of the surveyed trunks and used this in the analysis.

Fruiting longevity between morphologically different fungal groups was analyzed with Kruskal-Wallis one-way ANOVA. In the supplementary material we also provide the Nemenyi pairwise comparisons between the groups. The analyses were conducted in R (R Core Team, 2015).

3. Results

The taxon-specific information on timing and longevity of fruiting, fruit body size, substrate and number of occurrences is reported in the supplementary material (Appendix 2).

All groups except perennial polypores showed a seasonal pattern in their fruiting, agarics showing the highest and pyrenomycetes the lowest seasonality (Fig. 1A, Appendix 3). On average, perennial (129 d ± 20 SD) and annual polypores (80 ± 47), corticioids (89 ± 44) and pyrenomycetes (82 ± 36) had long, discomycetes (59 ± 36) intermediate, and agarics (26 ± 14) and jelly fungi (42 ± 27) the shortest mean fruiting longevity (Fig. 1B).

The longevity of fruiting was also statistically different between the morphological groups (Kruskal-Wallis ANOVA, $\chi^2 = 88.62$, $df = 6$, $P < 0.001$, Fig. 1B). The difference was mainly due to agarics having shorter fruiting longevity than the other groups. In addition, discomycetes tended to differ from perennial polypores and corticioids with shorter fruiting. Jelly fungi differed from the longest fruiting perennial polypores (Appendix 3).

4. Discussion

The detection level of fungal species is always in a tradeoff with focus given on other data qualities and, the optimal solution depends on the study question one is answering (Abrego et al., 2016). Regardless of the question, species' fruiting phenology is a key variable to consider in planning any survey scheme optimally.

In this study, surprisingly, one third of annual polypores and the majority of the corticioids were already fruiting by the first survey immediately after snow melt in May, in practice fruiting

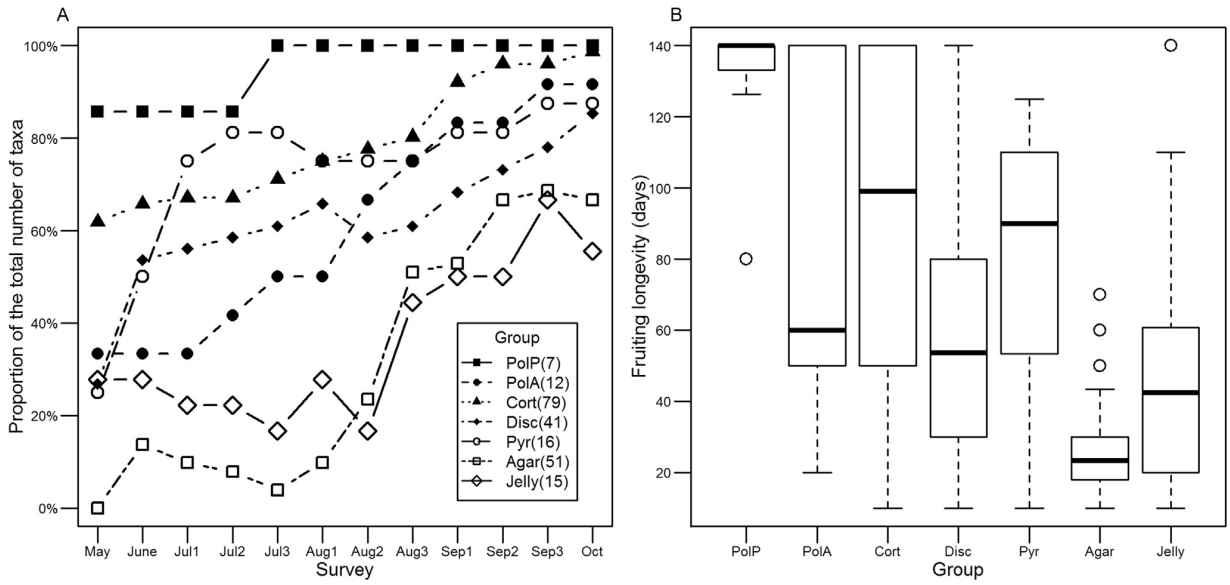

Fig. 1. (A) Taxa detected in each survey as a proportion of the total number of taxa detected during the whole study; and (B) longevity of fruiting, both split according to the different morphological groups (see methods for abbreviation explanations).

throughout the whole season. However, taxa with shorter fruiting longevity exist in these groups and new taxa were accumulating constantly as the study period exceeded. Thus, a minimum of two surveys, evenly distributed throughout the season would have allowed detection of the majority of the fruiting taxa of these groups.

The small proportions of taxa of discomycetes and pyrenomycetes detected during the first sampling occasion probably partly results from the untrained eye of the surveyor, not able to detect the taxa even though they were present (many of the species are extremely small). Thus, more reliable fruiting curves start from the second or third survey. This is a good example of challenges related to sampling the most difficult fungal groups. Discomycetes were fruiting longer than we expected (on average nearly two months), while for pyrenomycetes the long average fruiting longevity (somewhat less than three months) is not that surprising. Pyrenomycetes have very durable, hard, perithecial fruit bodies that can remain visible even for several years. This indicates that the guidelines for annual polypores and corticioids would also apply for pyrenomycetes. For discomycetes more surveys are needed to reach a similar detection level.

The agarics and jelly fungi had the most seasonal pattern in their fruiting, with the majority of the taxa producing fruit bodies after the summer months. These groups also had the shortest average fruiting longevity. When these results are combined, a guideline for a sufficient surveying approach for agarics and jelly fungi would be to conduct several surveys, as recommended for agarics also by Halme and Kotiaho (2012), and concentrate them towards the late season.

The present data are temporally and spatially limited. Hence, more occurrence specific fruiting phenology surveys are needed in the future to extend the findings of this study to other systems. For example, surveys covering multiple years and climatic zones would be ideal.

Acknowledgments

We thank Claus Bässler and an anonymous reviewer for their constructive comments about the manuscript. We also thank Karl-Henrik Larsson for providing some of the fruit body size measurements, Katja Juutilainen guiding the identification of corticioids, Ernest Emmett checking some *Mycena*-specimens and Noora Vartija helping with the data collection. This study was funded by Finnish Ministry of Environment, Societas pro Fauna et Flora Fennica, Vanamory and Vuokon luonnonsuojelusäätiö.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funeco.2016.06.007.

References

Abrego, N., Halme, P., Purhonen, J., Ovaskainen, O., 2016. Fruit body based inventories in wood-inhabiting fungi: should we replicate in space or time? Fungal Ecol. 20, 225–232.

Berglund, H., Edman, M., Ericson, L., 2005. Temporal variation of wood-fungi diversity in boreal old-growth forests: implications for monitoring. Ecol. Appl. 15, 970–982.

Dahlberg, A., Mueller, G.M., 2011. Applying IUCN red-listing criteria for assessing and reporting on the conservation status of fungal species. Fungal Ecol. 4, 147–162.

Dickie, I. a., Kałucka, I., Stasińska, M., Oleksyn, J., 2010. Plant host drives fungal phenology. Fungal Ecol. 3, 311–315.

Halme, P., Heilmann-Clausen, J., Rämä, T., Kosonen, T., Kunttu, P., 2012. Monitoring fungal biodiversity – towards an integrated approach. Fungal Ecol. 5, 750–758.

Halme, P., Kotiaho, J.S., 2012. The importance of timing and number of surveys in fungal biodiversity research. Biodivers. Conserv. 21, 205–219.

Halme, P., Vartija, N., Salmela, J., Penttinen, J., Norros, V., 2013. High within- and between-trunk variation in the nematoceran (Diptera) community and its physical environment in decaying aspen trunks. Insect Conserv. Divers 6, 502–512.

Kéry, M., Spillmann, J.H., Truong, C., Holderegger, R., 2006. How biased are estimates of extinction probability in revisitation studies? J. Ecol. 94, 980–986.

Löhmus, A., 2009. Factors of species-specific detectability in conservation assessments of poorly studied taxa: the case of polypore fungi. Biol. Conserv. 142, 2792–2796.

Moore, D., Gange, A.C., Gange, E.G., Boddy, L., 2008. Fruit bodies: their production and develpoment in relation to environment. In: Boddy, L., Frankland, J.C., van West, P. (Eds.), Ecology of Saprotrophic Basidiomycetes. Elsevier, London, pp. 79–102.

Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., Nordén, J., 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. ISME J. 7, 1696–1709.

R Core Team, 2015. R: a Language and Environment for Statistical Computing.

Renvall, P., 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35, 1–51.

Royal Botanic Gardens Kew, Landcare Research-NZ, Chinese Academy of Science, 2015, Index Fungorum [WWW Document], www.indexfungorum.org

van der Linde, S., Holden, E., Parkin, P.I., Alexander, I.J., Anderson, I.C., 2012. Now you see it, now you don't: the challenge of detecting, monitoring and conserving ectomycorrhizal fungi. Fungal Ecol. 5, 633–640.

Detailed information on fruiting phenology provides new insights on wood-inhabiting fungal detection

Jenna Purhonen, Seppo Huhtinen, Heikki Kotiranta, Janne S. Kotiaho & Panu Halme

Appendix 1.

The monitoring procedure

Every occurrence (fruit body or fruit body group) was marked with pins and number labels to enable the tracking of the longevity of the fruiting without a need to collect repeated specimens. We also draw a fruit body map of each trunk to support the monitoring and to ensure that we were able to detect the whole fruiting event during every survey (for example in cases when fruit bodies of one species were very scattered along the trunk surface (Figure S1). The bark or moss cover was not removed nor were the trunks turned over to enable the following monitoring without major changes on the trunk surface.

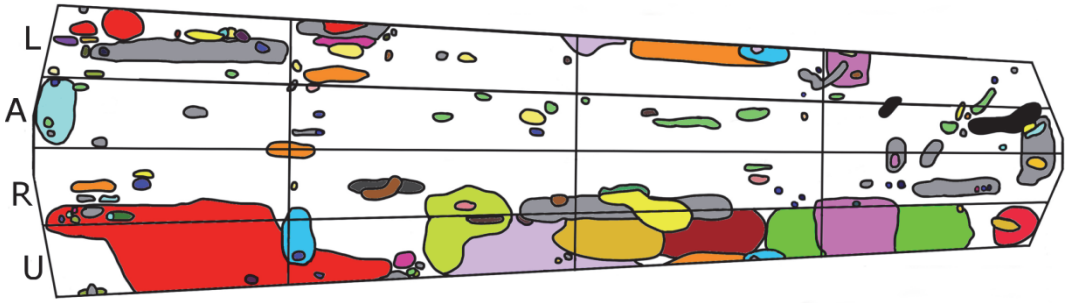

Figure S1. All fruit body occurrences detected during the whole study period (12 surveys) illustrated on a trunk map drawn from one of the study birches. The surface of the trunk is spread open and divided into four horizontal segments; above side (A), left side (L), right side (R) and under side (U) as well as lengthwise into four equally long segments. Each colour illustrates one taxon.

Detailed information on fruiting phenology provides new insights on wood-inhabiting fungal detection

Jenna Purhonen, Seppo Huhtinen, Heikki Kotiranta, Janne S. Kotiaho & Panu Halme

Appendix 2.

Species specific information

Data shown for the detected taxa of each morphological group in alphabetical order. Timing of fruiting and its standard deviation (SD), reported as mean of the surveys when fruiting started. Longevity of fruiting and its standard deviation (SD), reported as mean number of fruiting days. The fruit body size (in millimeters), based on averages of the measures given in the following literature or by species experts. The thickness of the fruit body was considered as the measure of size for perennial and annual polypores, corticioids and heterobasidiomycetes (Eriksson and Ryvarden, 1973-1976; Eriksson et al., 1978-1984; Hansen and Knudsen, 1997; Niemelä, 2005, personal communication with Karl Henrik Larsson and our own experience). For the agarics, the size measure was the diameter of the cap (Knudsen and Vesterholt, 2008) and for disco- and pyrenomycetes the diameter of the apothecia (Baloch et al., 2009; Breitenbach and Kränzlin, 1984; Hansen and Knudsen, 2000; Raitviir, 2004 and our own experience). Tree species the taxon inhabited; B = birch, P = Scots pine, B/P = both. N = number of observations for each taxon. If the taxon inhabited both birch and pine, timing, longevity and n are given separately for both tree species.

Perennial polypores	**Timing**	**Longevity**	**Size**	**Tree**	**N**
Fomes fomentarius	May±0	140±0	120	B	5
Fomitopsis pinicola	June±3/May±0	123±45/133±13	45	B/P	7/4
Perenniporia subacida	Jul3	80	10	P	1
Phellinus igniarius coll.	May	140	80	B	1
Phellinus laevigatus	May	140	7,5	B	1
Phellinus lundellii	May	140	12,5	B	1
Phellinus viticola	May	140	7,5	P	1
Annual polypores	**Timing**	**Longevity**	**Size**	**Tree**	**N**
Amyloporia sinuosa	May±0	140±0	3	P	6
Ceriporia excelsa	May	140	1	B	1
Flaviporus citrinellus	Sep3	20	1,25	B	1
Ischnoderma benzoinum	Aug3	50	15	P	1
Postia caesia	Sep2	30	5	B	1
Postia fragilis	Aug2	60	17,5	P	1
Postia tephroleuca	Sep1/Sep3	40/20	7,5	B/P	1/1
Rhodonia placenta	Aug2	60	3,5	P	1
Skeletocutis biguttulata	May±0	140±0	2	P	4
Skeletocutis nivea	May	140	3,5	B	1
Skeletocutis papyracea	Jul2	60	1	P	1
Skeletocutis sp.	May	140	2,17	P	1
Trichaptum abietinum	Jul3	80	3	P	1
Corticioids	**Timing**	**Longevity**	**Size**	**Tree**	**N**
Amyloxenasma cf. grisellum	May	140	0,0375	P	1
Aphanobasidium pseudotsugae	Jul1±3	115±44	0,03	P	6
Athelia decipiens	Jul3±5/Jul1±3	83±54/113±38	0,085	B/P	3/3
Athelia epiphylla coll.	Jul3±4	55±15	0,11	B	2
Athelia neuhoffii	May±0/May±0	80±54/83±59	0,11	B/P	3/6

Athelia sp.	Jul1±4/Aug1±5	94±54/15±5	0,102	B/P	5/2
Basidiodendron caesiocinereum	Sep2	30	0,09	B	1
Botryobasidium botryosum	Jul1±2/May±0	78±38/133±13	0,155	B/P	4/4
Botryobasidium conspersum	Jul1	100	0,085	B	1
Botryobasidium medium	Sep1/Aug1	40/70	0,155	B/P	1/1
Botryobasidium subcoronatum	Jul3±4/Jul1±3	95±45/110±33	0,155	B/P	2/5
Botryobasidium sp.	May	120	0,1375	P	1
Botryohypochnus isabellinus	Aug1±3	80±35	0,155	B	4
Ceraceomyces microsporus	May	140	0,25	P	1
Ceraceomyces tessulatus	Oct/May	10/70	0,3	B/P	1/1
Coniophora arida	Sep3	20	0,3	P	1
Coniophora olivacea	Sep1	40	0,3	B	1
Coniophora puteana	Oct	10	1,25	P	1
Crustoderma corneum	May±0	140±0	0,5	P	2
Dacryobolus karstenii	May	140	0,75	P	1
Gloeocystidiellum convolvens	May	140	0,3	B	1
Gloeodontia subasperispora	May	140	0,075	P	1
Hastodontia hastata	May	140	0,15	P	1
Hymenochaete fuliginosa	Jul3	60	0,35	P	1
Hyphoderma definitum	May	140	0,05	P	1
Hyphoderma incrustatum	Sep2	30	0,1	B	1
Hyphoderma setigerum coll.	Aug1±3	67±33	2,55	B	3
Hyphoderma sp.	Jul2±0	55±35	0,1	B	2
Hyphodontia abieticola	Jul2±3	75±65	0,75	P	2
Hyphodontia alienata	June	110	0,1	B	1
Hyphodontia pallidula	June	110	0,15	B	1
Hyphodontia subalutacea	May±0/Sep2	140±0/30	0,1	B/P	3/1
Hyphodontia sp.	May	140	0,29	P	1
Hypochnicium geogenium	Sep2	30	0,2	P	1
Hypochnicium punctulatum	Sep3±1	50±10	0,2	P	2
Hypochnicium subrigescens	Sep1	40	0,2	B	1
Kurtia argillacea	Aug3±1	50±10	0,15	B	2
Leucogyrophana romellii	Sep3	20	0,25	P	1
Merulius tremellosus	Aug3	50	3	B	1
Mucronella calva	Aug1±3	67±31	1,75	B	3
Mycoacia fuscoatra	Jul3±4	95±45	1,35	B	2
Peniophora incarnata	June±1	115±26	0,2	B	4
Peniophora laurentii	May	10	0,35	B	1
Peniophora violaceolivida	June±2	123±30	0,2	B	4
Peniophorella pallida	Aug2	60	0,1	P	1
Peniophorella praetermissa coll.	Sep1/Aug1±5	40/80±60	0,1	B/P	1/2
Phanerochaete cretacea	May±0	140±0	0,125	P	4
Phanerochaete laevis	Aug3/Aug1	50/70	0,4	B/P	1/1
Phanerochaete sordida coll.	May	140	0,35	B	1
Phanerochaete velutina	May±0	140±0	0,3	B	3
Phlebia deflectens	Jul3	50	0,15	B	1
Phlebia cf. lilascens	Aug1	70	0,25	P	1
Phlebia rufa	Sep1	40	1,1	B	1
Phlebia segregata	May	140	0,15	P	1
Phlebia serialis	May±0	130±14	0,125	P	3

Pseudochaete tabacina	Aug1	70	0,45	B	1
Pseudomerulius aureus	May	140	1,5	P	1
Resinicium bicolor	June/May	110/140	0,425	B/P	1/1
Resinicium furfuraceum	May±0	140±0	0,125	P	6
Rhizoctonia fusisporus	Jul1	100	0,15	B	1
Scytinostroma galactinum	June±1	125±15	1,5	B	2
Serpula himantioides	Sep1	40	2	P	1
Sistotrema cf. binukleosporum	May	140	0,04	P	1
Sistotrema brinkmannii	May	40	0,125	B	1
Sistotrema raduloides	May	140	2,05	B	1
Sistotrema resinicystidium	May±0	113±31	0,15	B	3
Sistotrema sp.	May	10	0,105	B	1
Stereum hirsutum	May±0	140±0	1,5	B	4
Stereum rugosum	Jul2±4	107±47	3	B	3
Tomentella sp.	Sep3±1	23±12	-	B	3
Trechispora cf. farinacea	May	140	0,525	P	1
Trechispora subsphaerospora	Jul2	90	0,125	P	1
Tubulicrinis borealis	Jul3	80	0,085	P	1
Tubulicrinis calothrix	May/May±0	140/140±0	0,175	B/P	1/5
Tubulicrinis medius	May±0	140±0	0,15	P	2
Tubulicrinis propinquus	Sep1	40	0,05	P	1
Tubulicrinis strangulatus	May	140	0,075	P	1
Tubulicrinis subulatus	May±0	134±12	0,15	P	5
Tubulicrinis sp.	May±0	140±0	0,114	P	2
Tulasnella eichleriana	Sep1	40	0,075	B	1
Tulasnella violea	June±1	60±50	0,075	B	2
Tulasnella sp.	Sep3	20	0,075	B	1
Xenasmatella vaga	Sep1	40	0,3	P	1
Xylodon asperus	May	140	0,4	P	1
Xylodon brevisetus	Jul1±3	110±40	0,5	P	5
Xylodon rimosissimus	May	140	0,2	B	1
Discomycetes	**Timing**	**Longevity**	**Size**	**Tree**	**N**
Arachnopeziza aurata	June±0	43±19	0,6	B	4
Arachnopeziza sp1.	June±1	67±24	0,675	P	3
Arachnopeziza sp2.	Jul2±3	61±46	0,75	B	7
Ascocoryne sp.	Aug3±2/Sep2±0	52±21/30±0	1,25	B/P	5/2
Bisporella citrina	Aug1±1	66±14	1,75	B	7
Capitotricha bicolor	May±0	130±14	1,25	B	3
Ciliolarina neglecta	Sep3±1	20±10	0,25	P	2
Claussenomyces atrovirens	Aug1/Jul2±4	70/86±38	1	B/P	1/5
Cryptodiscus pini	May	140	0,45	P	1
Discomycetes sp.	Aug1	10	-	B	1
Discomycetes sp1.	Jul1	10	-	B	1
Discomycetes sp2.	Aug1	70	-	B	1
Durella cf. atrocyanea	Sep1	40	1	P	1
Durella melanochlora	June±1	120±20	0,6	B	2
Gyromitra infula	Sep2±1	35±5	80	B	2
Humaria hemisphaerica	Aug2±5	30±20	17,5	B	2
Hyaloscypha albohyalina var. albohyalina	June/Jul2	110/80	0,45	B/P	1/1

Hyaloscypha aureliella	Aug2±4	58±42	0,8	P	8
Hyaloscypha vitreola	Aug2±5	60±50	0,4	B	2
Hymenoscyphus cf.salicellus	Oct	10	1,5	B	1
Hymenoscyphus sp1.	Sep1±0	15±5	1,5	B	2
”Hyphodiscus hemiamyloideus”	Aug3	50	0,45	B	1
Lachnum papyraceum	Sep2	30	0,75	B	1
Lachnum virgineum	June±0	77±34	1,25	B	6
Lachnum sp1.	Jul2±4	43±19	1,08	B	4
Leptodontidium trabinellum	Oct±0	12±4	0,65	B	5
Mollisia sp1.	Jul1±2/Jul3±4	94±36/76±36	2	B/P	13/9
Mollisia sp2.	Aug1±4	46±36	2	B	7
Mollisia sp3.	June	30	2	P	1
Mollisia sp4.	Jul1	80	2	P	1
Neobulgaria lilacina	June	100	1,25	B	1
Neodasyscypha cerina	Jul2	40	0,75	B	1
Orbilia cf. delicatula	Jul3±2/Jul2±1	70±24/80±33	0,75	B/P	4/5
Orbilia cf. inflatula	Jul1±1	83±21	1	B	3
Orbilia cf. xanthostigma	Jul2	65	0,6	B	2
Patinellaria sanguinea	Jul3	80	0,4	B	1
Phaeohelotium sp1.	Sep3	20	0,65	B	1
Propolis farinosa	June±1	118±18	3,5	B	5
Pseudoplectania nigrella	May	10	17,5	B	1
Psilocistella cf. obsoleta	Oct	10	0,1	B	1
Scutellinia scutellata	May	140	9	B	1
Strossmayeria basitricha	Sep3	20	0,5	B	1
Pyrenomycetes	**Timing**	**Longevity**	**Size**	**Tree**	**N**
Annulohypoxylon multiforme	June±1	120±18	25	B	7
Bertia moriformis	June±1	125±15	0,5	P	2
Chaetosphaeria ovoidea	June	110	0,35	B	1
Hysterium pulicare	Sep1±0	40±0	0,75	B	2
Lasiosphaeria ovina	Jul1±0	70±30	0,5	B	2
Lasiosphaeria sp1.	Jul3±2	67±24	0,5	B	3
Lasiosphaeria sp2.	June	40	0,5	B	1
Lophiostoma compressum	June	110	0,8	B	1
Lophium mytilinum	Jul2±1	90±8	1,5	P	3
Melanomma pulvis-pyrius	Jul1	100	0,4	B	1
Pyrenomycetes sp1.	Jul2±2	90±20	-	B	2
Pyrenomycetes sp2.	June	110	-	B	1
Pyrenomycetes sp3.	Jul2	90	-	B	1
Pyrenomycetes sp4.	June±1	117±17	-	B	2
Pyrenomycetes sp5.	May	10	-	B	1
Trichoderma pulvinatum	Sep3	20	11	B	1
Agarics	**Timing**	**Longevity**	**Size**	**Tree**	**N**
Armillaria borealis	Sep2±3	18±7	65	B	6
Cheimonophyllum candidissimum	Aug3	50	10	B	1
Clitopilus hobsonii	Sep2	30	8,5	B	1
Crepidotus versutus	Sep2	30	15	B	1
Flammulaster limulatoides	Aug3	20	24	B	1
Galerina atkinsoniana	Sep2±2	25±5	6,5	B	2

Galerina cephalotricha	Sep3/Aug1±3	20/30±16	10	B/P	1/3
Galerina hypnorum	Sep2/Sep2	10/10	10	B/P	1/1
Galerina marginata	Sep3±0	20±0	17,5	B	2
Galerina mniophila	Sep3±1	15±9	10	B	4
Galerina pumila	Sep3	20	14	P	1
Galerina vittiformis	Sep2	10	12,5	B	1
Galerina sp.	Sep1±2/Sep2±1	18±12/23±13	10,96	B/P	5/7
Gymnopilus penetrans	Sep2±1/Sep1±1	30±10/38±11	50	B/P	2/4
Gymnopilus picreus	Sep2	30	22,5	P	1
Gymnopus sp.	Jul3	20	-	P	1
Hohenbuehelia auriscalpium	Aug2	60	22,5	B	1
Hypholoma capnoides	Sep3/Oct	20/10	42,5	B/P	1/1
Kuehneromyces lignicola	Jul1	60	25	B	1
Kuehneromyces mutabilis	Aug3	50	30	B	1
Kuehneromyces sp.	Jul1	10	27,5	B	1
Lactarius camphoratus	Jul3	60	35	B	1
Lactarius tabidus	Sep1±2	23±12	25	B	3
Lactarius vietus	Aug3	40	47,5	B	1
Lactarius sp.	Aug3	10	35,8	B	1
Lentinellus cf. ursinus	Aug3	50	47,5	B	1
Mycena algeriensis	Aug2±3	25±25	20	B	6
Mycena epipterygia	Sep3±0	20±0	20	P	3
Mycena flavoalba	Sep3	10	12,5	B	1
Mycena galericulata	Sep2±1	30±12	27,5	B	4
Mycena haematopus	Sep1±1	27±9	20	B	3
Mycena laevigata	Aug3	30	20	P	1
Mycena metata	Sep2±1/Sep3±0	26±8/18±4	15	B/P	10/5
Mycena niveipes	June	10	37,5	B	1
Mycena pura	Aug3	20	30	B	1
Mycena rubromarginata	Sep2±1/Aug3±3	23±12/33±35	15	B/P	3/6
Mycena sanguinolenta	Aug3±0/Sep1	17±5/20	10	B/P	3/1
Mycena stipata	Aug3±2	43±14	20	P	9
Mycena tintinnabulum	Sep2±0	33±4	25	B	4
Mycena viridimarginata	Sep2±2	13±5	23	P	3
Mycena sp.	Sep2±1/Aug3±2	19±8/19±7	18,56	B/P	7/10
Pholiota sp1.	Sep2	30	60	B	1
Pholiota sp2.	Jul2	10	60	B	1
Pholiota tuberculosa	Aug3	20	60	B	1
Pluteus cervinus	Aug3±1	31±14	85	B	7
Pluteus semibulbosus	Sep2	10	35	B	1
Resupinatus poriaeformis	Aug1	70	0,7	B	1
Rhizomarasmius setosus	Aug3	10	2,75	B	1
Roridomyces roridus	Sep3±0/Sep2	24±5/30	6	B/P	5/5
Simocybe centunculus	Aug2±1	20±0	12,5	B	2
Tricholomopsis decora	Aug2	60	42,5	P	1
Tubaria conspersa	Sep2	30	13	B	1
Tubaria furfuracea	June/Sep2±1	10/30±10	21,5	B/P	1/2
Tubaria sp.	Sep3	20	17,25	B	2
Xeromphalina campanella	Oct	10	12	P	1
Xeromphalina picta	June	20	4	B	1

Jelly fungi	Timing	Longevity	Size	Tree	N
Calocera cornea	Aug3±0	47±5	7,5	B	3
Cerinomyces crustulinus	May	140	0,1	P	1
Dacrymyces cf. microporus	Sep3	20	5	P	1
Dacrymyces enatus	June±1	30±20	2	B	2
Dacrymyces lacrymalis	Jul3±3	47±39	3	B	3
Dacrymyces stillatus	June	110	3	P	1
Dacrymyces tortus	Aug3±2	51±18	1	P	7
Dacrymyces sp.	Sep3/Jul3	20/70	1,76	B/P	1/1
Ditiola peziziformis	Sep1	40	7,5	B	1
Exidia glandulosa	June	10	30	B	1
Exidia saccharina	Jul2	80	60	P	1
Jelly fungi sp1.	May	70	-	B	1
Jelly fungi sp2.	Sep3	20	-	B	1
Jelly fungi sp3.	May	10	-	B	1
Jelly fungi sp4.	June	30	-	P	1
Tremella foliacea	Sep3	20	75	B	1

References

Baloch, E., Gilenstam, G., Wedin, M., 2009. Phylogeny ans classification of Cryptodiscus, with taxonimic synopsis of the Swedish species. Fungal Divers. 38, 51–68.

Breitenbach, J., Kränzlin, F., 1984. Fungi of Switzerland: Ascomycetes, Vol. 1. Verlag Mykologia, Luzern.

Eriksson, J., Hjortstam, K., Ryvarden, L., 1978-1984. The Corticiaceae of North Europe, Vols. 5, 6, 7. Fungiflora, Oslo.

Eriksson, J., Ryvarden, L., 1973-1976. The Corticiaceae of North Europe, Vols. 2, 3, 4. Fungiflora, Oslo.

Hansen, L., Knudsen, H., 2000. Nordic Macromycetes: Ascomycetes, Vol. 1. Nordsvamp, Copenhagen.

Hansen, L., Knudsen, H., 1997. Nordic Macromycetes: Heterobasidioid, Aphyllophoroid and Gastromycetoid Basidiomycetes, Vol.3. Nordsvamp, Copenhagen.

Knudsen, H., Vesterholt, J., 2008. Funga Nordica. Nordsvamp, Copenhagen.

Niemelä, T., 2005. Käävät, puiden sienet. Norrlinia 13, 1–320.

Raitviir, A., 2004. Revised synopsis of the Hyaloscyphaceae. Scr. Mycol. 20, 1–132.

Detailed information on fruiting phenology provides new insights on wood-inhabiting fungal detection

Jenna Purhonen, Seppo Huhtinen, Heikki Kotiranta, Janne S. Kotiaho & Panu Halme

Appendix 3.

Supplementary results

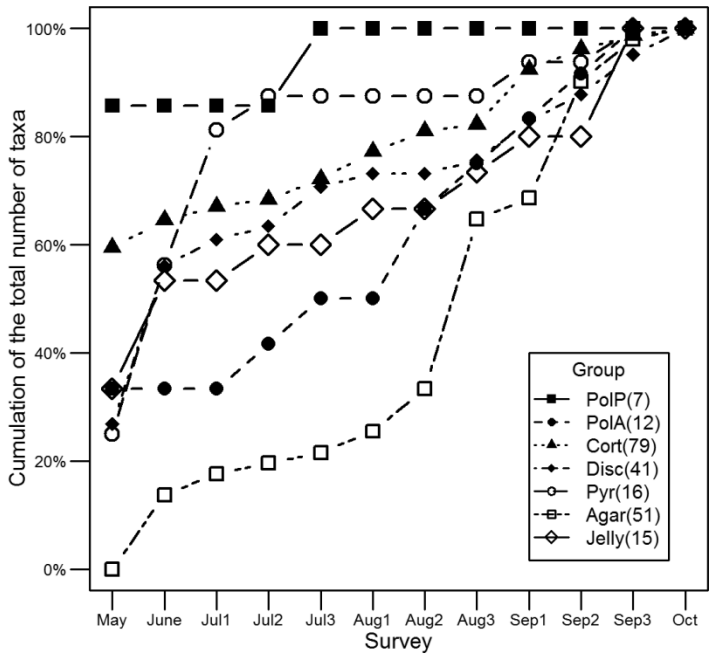

Figure S2. Accumulation of the total number of taxa at each survey occasion of the different morphological groups; perennial polypores (PolP), annual polypores (PolA), corticioids (Cort), discomycetes (Disc), pyrenomycetes (Pyr), agarics (Agar) and jelly fungi (Jelly).

Table S1. The p-values of Nemenyi pairwise comparisons of fruiting longevity, with Chi-squared approximation for independent samples, between morphological fungal groups (perennial polypores (PolP), annual polypores (PolA), corticioids (Cort), discomycetes (Disc), pyrenomycetes (Pyr), agarics (Agar) and jelly fungi (Jelly)).

	PolP	PolA	Cort	Disc	Pyr	Agar
PolA	0.769	–	–	–	–	–
Cort	0.719	1.000	–	–	–	–
Disc	0.063	0.796	0.058	–	–	–
Pyr	0.657	1.000	1.000	0.837	–	–
Agar	0.000	0.005	0.000	0.029	0.003	–
Jelly	0.042	0.622	0.105	0.997	0.666	0.725

II

DEAD WOOD PROFILE OF A SEMI-NATURAL BOREAL FOREST - IMPLICATIONS FOR SAMPLING

by

Halme Panu, Purhonen Jenna, Marjakangas Emma-Liina, Komonen Atte, Juutilainen Katja & Abrego Nerea 2018

Submitted manuscript

Request a copy from author.

III

EFFECTS OF LOCAL FOREST CONTINUITY ON THE DIVERSITY OF FUNGI ON STANDING DEAD PINES

by

Saine Sonja, Aakala Tuomas, Purhonen Jenna, Launis Annina, Tuovila Hanna, Kosonen Timo & Halme Panu 2018

Forest Ecology and Management 409: 757–765.

Forest Ecology and Management 409 (2018) 757–765

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of local forest continuity on the diversity of fungi on standing dead pines

Sonja Saine[a,*], Tuomas Aakala[b], Jenna Purhonen[a], Annina Launis[c], Hanna Tuovila[a], Timo Kosonen[d], Panu Halme[a]

[a] Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 University of Jyväskylä, Finland
[b] Department of Forest Sciences, University of Helsinki, P.O. Box 27, FI-00014 University of Helsinki, Finland
[c] Botany Unit, Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland
[d] Herbarium, Biodiversity Unit, University of Turku, FI-20014 Turku, Finland

ARTICLE INFO

Keywords:
Dead wood continuity
Decomposer
Micarea
Microhabitat continuity
*Pinus sylvestris*L.
Stand continuity

ABSTRACT

Human-induced fragmentation affects forest continuity, i.e. availability of a suitable habitat for the target species over a time period. The dependence of wood-inhabiting fungi on landscape level continuity has been well demonstrated, but the importance of local continuity has remained controversial. In this study, we explored the effects of local forest continuity (microhabitat and stand level) on the diversity of wood-inhabiting fungi on standing dead trunks of Scots pine (*Pinus sylvestris* L.). We studied species richness and community composition of decomposers and *Micarea* lichens on 70 trunks in 14 forests in central Finland that differed in their state of continuity. We used dendrochronological methods to assess the detailed history of each study trunk, i.e. the microhabitat continuity. The stand continuity was estimated as dead wood diversity and past management intensity (number of stumps). We recorded 107 species (91 decomposers, 16 *Micarea* lichens), with a total of 510 occurrences. Using generalized linear mixed models, we found that none of the variables explained decomposer species richness, but that *Micarea* species richness was positively dependent on the time since tree death. Dead wood diversity was the most important variable determining the composition of decomposer communities. For *Micarea* lichens, the community composition was best explained by the combined effect of years from death, site and dead wood diversity. However, these effects were rather tentative. The results are in line with those of previous studies suggesting the restricted significance of local forest continuity for wood-inhabiting fungi. However, standing dead pines that have been available continuously over long periods seem to be important for species-rich communities of *Micarea* lichens. Rare specialists (e.g. on veteran trees) may be more sensitive to local continuity, and should be at the center of future research.

1. Introduction

Intensive forestry activities have led to severe forest fragmentation throughout the globe (Riitters et al., 2000). The spatial aspects of fragmentation, such as decreased habitat amount, size, and connectivity are well known for a negative effect on biodiversity and ecosystems (Bengtsson et al., 2000; Fahrig, 2003). Temporal aspects of fragmentation, such as decreased habitat continuity, have been studied less than the spatial aspects, but have similarly been shown to have negative impacts on biodiversity (Nordén et al., 2014).

Forest continuity can be considered at local level where it relates to longevity of a single, available patch of suitable habitat for the target species or community, and where the scale of habitat patch is equivalent to one local population (Hanski, 2005; Nordén et al., 2014). With higher local continuity, higher species richness and larger variety of specialist species can occur as the colonization and/or breeding probability of species with establishment constraints, slow rates of establishment, development, or growth is enhanced (Esseen et al., 1997; Fritz et al., 2008; Nilsson and Baranowski, 1997; Nordén et al., 2014). The cause for higher species richness and larger variety of specialists may also be the emergence of special microhabitat types confined to late successional phases or larger diversity of different microhabitats. This is due to the absence of large-scale disturbances, which promotes the time-demanding development of these resources (Tibell, 1992; Sverdrup-Thygeson, 2001; Winter and Möller, 2008). Landscape level continuity, on the other hand, refers to a network of available habitat patches within a given region or landscape over time (Fritz et al., 2008; Hanski, 2005; Nordén et al., 2014). Here, the role of dispersal

* Corresponding author.
E-mail address: sonja.saine@gmail.com (S. Saine).

https://doi.org/10.1016/j.foreco.2017.11.045
Received 28 June 2017; Received in revised form 21 November 2017; Accepted 22 November 2017
Available online 22 December 2017
0378-1127/

limitations increases when the landscape level continuity decreases (Nordén and Appelqvist, 2001).

Wood-inhabiting fungi are among the organism groups suffering most from the decreased landscape level forest continuity caused by fragmentation (Nordén et al., 2014; Flensted et al., 2016). The importance of this landscape level continuity for wood-inhabiting fungal diversity has been well demonstrated (Flensted et al., 2016; Gu et al., 2002; Junninen and Komonen, 2011; Paltto et al., 2006; Ranius et al., 2008; Sverdrup-Thygeson and Lindenmayer, 2003). Apparently, the biological reason for this dependence is that some species of wood-inhabiting fungi are in fact dispersal limited (e.g. Norros et al., 2012), although species dependent on ephemeral habitats have a high dispersal ability in general (Herben et al., 1991).

The role of local continuity has remained less clear, compared to landscape level continuity. Stokland and Kauserud (2004) suggested that a polypore *Phellinus nigrolimitatus* cannot effectively colonize suitable trunks when the stand level dead wood continuity decreases. With epiphytic lichens, forest age and continuity appear to have a positive effect on their species richness and affect their community composition (Fritz et al., 2008). Also here, the increased colonization probability with increasing forest age and continuity was considered as the most probable explanation. On the other hand, several studies have detected no effects of local continuity (Groven et al., 2002; Rolstad et al., 2004; Sverdrup-Thygeson and Lindenmayer, 2003), and many studies have been criticized for not demonstrating the effect of continuity *per se* (Nordén and Appelqvist, 2001; Nordén et al., 2014).

In their review, Junninen and Komonen (2011) deduced that boreal polypores are not affected by continuity on a stand scale in any way, and Nordén et al. (2014) concluded that local continuity does not have a significant effect on the diversity of fungi. Nevertheless, this generalization may be misleading; fungi encompass species with divergent ecological characteristics, with many of the species being habitat specialists, requiring dead wood in advanced stages of decay (Nordén et al., 2013). Moreover, studies have not focused on the smallest scale of local continuity, i.e. the detailed history of the microhabitats. Especially the standing dead coniferous trees may retain their qualities for decades, and therefore constitute a microhabitat with potentially high continuity. Considering ephemeral habitats in general, standing dead coniferous trees may be among the slowest constantly changing microhabitats (compared to more persistent abiotically determined microhabitats, such as those in soil).

In this study, we explored the effects of local forest continuity (microhabitat and stand level) on the communities of wood-inhabiting fungi. We studied fungal communities on standing dead wood of Scots pine (*Pinus sylvestris* L., hereafter pine) in 14 forests with varying state of continuity. We used trunk age parameters as estimates for microhabitat continuity, and estimated stand continuity as dead wood diversity and past management intensity. We focused on pine because the species is characterized by slow death and decay process (Niemelä et al., 2002; Siitonen, 2001). Specifically, we asked:

1. How does local forest continuity affect (i) species richness and (ii) community composition of wood-inhabiting fungi inhabiting standing dead pines?
2. How different scales of continuity (from microhabitat continuity to stand continuity) affect (i) species richness and (ii) community composition?
3. Are the effects of local continuity different for different fungal groups?

2. Materials and methods

2.1. Study sites and trunk selection

Our 14 study forests (Table 1) were located in central Finland (Fig. 1), 12 of them being in the southern boreal zone, and two in the middle boreal zone (Ahti et al., 1968). In each forest, the study trunks were selected on a 10-m wide transect. Each transect was established 15 m from the point of easiest access into the study stand. The direction of the transect was towards the center of the stand, except in smaller stands (< 100 m wide) where the transect followed the direction of the longest side of the stand. If the opposite side of a stand was met before trunks were surveyed, the transect was turned around and continued parallel to the first transect. The first five pine trunks within a transect that fulfilled the criteria of being (1) standing (leaning max. 45°) and dead, (2) trunks or high stumps (≥0.5 m in height), and (3) ≥7 cm in diameter, were selected for sampling.

Table 1
Site information. Dominant tree species and mean age classes are derived from Natural Resources Institute Finland (2015).

	Site	Municipality	Dominant tree species	Mean age class
1	Hallinmäki	Jämsä	spruce	96–132
2	Ilmakkamäki	Suonenjoki	pine	56–65
3	Kalaja	Rautalampi	pine	62–71
4	Kirkkokangas	Muurame	spruce	85–109
5	Kivetty	Äänekoski	spruce	72–84
6	Kotinen	Hämeenlinna	spruce	75–89
7	Kuusimäki	Muurame	spruce	45–55
8	Latokuusikko	Kuhmoinen	spruce	88–108
9	Leivonmäki	Joutsa	pine	62–78
10	Lortikka	Kuhmoinen	spruce	70–80
11	Pyhä-Häkki	Saarijärvi	pine	101–144
12	Vaarunvuoret	Jyväskylä	spruce	62–72
13	Vesijako	Padasjoki	spruce	54–63
14	Vuorilampi	Toivakka	pine	45–55

2.2. Data collection and preparations

2.2.1. Species data

All decomposer fungi and *Micarea* lichens were recorded from each study trunk based on the occurrence of fruit bodies. Sampling of *Micarea* and *Mycocaliciales* species was conducted in three parts: October 2014, May–June 2015, and September 2015. Rest of the groups (agarics, corticioids, discomycetes, jelly fungi, polypores, and pyrenomycetes) were sampled in separate surveys in August–September 2015. Agarics were sampled again during October 2015 to meet a better share of a local species community (their detectability is lower than in other groups, see Abrego et al. (2016) and Purhonen et al. (2016)). The trunks were carefully examined throughout from ground level up to a height of 1.8 m. Species of *Mycocaliciales* were recorded only from sapwood, all other fungal groups also from bark. Fungi were identified to species in the field if possible. Otherwise, specimens were taken for later microscopical identification in the laboratory. Species nomenclature followed Coppins (1983), Czarnota (2007), and Czarnota and Guzow-Krzemínska (2010) with *Micarea* species, Tibell (1999) with species of *Mycocaliciales*, and Index Fungorum (Royal Botanic Gardens Kew et al., 2016) with the rest. If possible, identifications were made to species level, otherwise to genus level.

In the analyses, we used species level identifications. We also included genus level identifications that were different from the identified species of the same genus. We have thoroughly aimed at a similar taxonomic resolution throughout the data. In the case of taxonomically very poorly known groups of *Chaenothecopsis* and *Mycocalium*, several undescribed species were separated based on spore size, type and some other anatomical and chemical characters, and considered as distinct species. Also, some pyrenomycetes remained unidentified, but when it was possible to separate them from the rest of the detected species, they were considered as species in the analyses.

2.2.2. Study trunk specific measures

Several variables were recorded for each study trunk in the field.

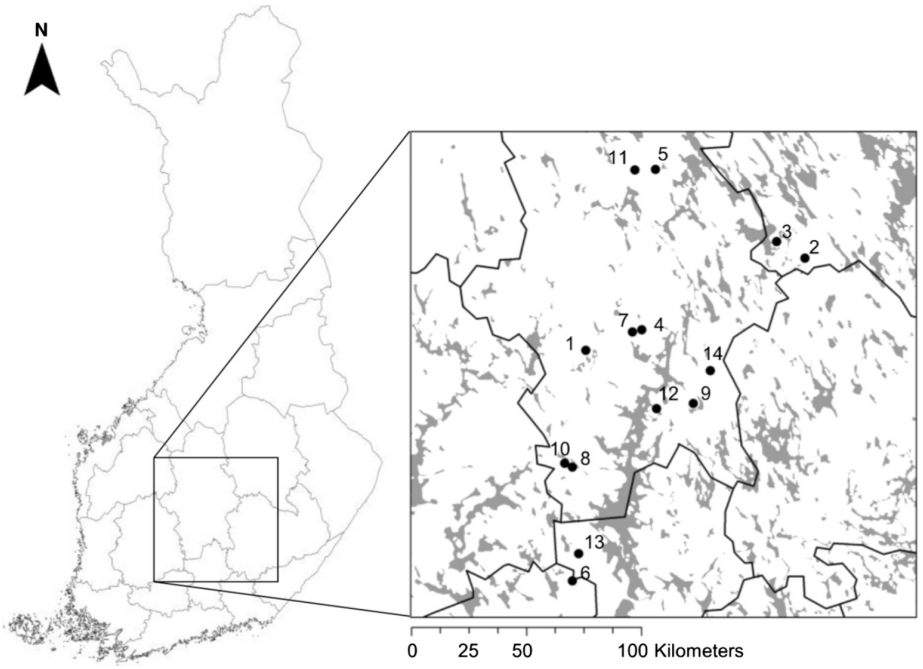

Fig. 1. The map showing the regions of Finland and the locations of the study sites. Site names are presented in Table 1. © National Land Survey of Finland 2016, 2017.

These included coordinates, circumference at breast height (cm), height (m), decay stage (1–5), the proportion of surface not covered by bark (%) and the coverage of lichens (%). The circumference at breast height was converted to diameter, and it was used as an estimate of survey effort.

We also estimated the canopy openness around the trunks. Four fisheye photos were taken towards principal compass points while standing back against the trunk. The proportion of visible sky was calculated from each photo, using ImageJ (version 1.45 s; Schneider et al., 2012). The final estimate for canopy openness was the mean of these four, trunk specific values.

2.2.3. Age and time since death of study trunks

We assigned each study trunk age and time since death, using dendrochronological methods. From each trunk, we extracted a cross-sectional sample disc, or a partial disc. When possible, the samples were extracted from the part of the trunk where bark was still present, to ensure we had the last growth ring. When bark or bark remnants were no longer present, we extracted the sample from where we subjectively estimated minimum ring erosion. In addition to the study trunks, we further extracted increment cores from five live trees within the vicinity of the study trunks at each site, for building a master chronology. In the laboratory, the samples were first dried, increment cores mounted to core mounts, and frail sample discs reinforced following Krusic and Hornbeck (1989; but in normal air pressure). Samples were sanded to make annual rings and ring borders clear and easily observable.

Tree rings were dated, using visual cross-dating (Yamaguchi, 1991), against the site-specific marker rings obtained from the live trees. The widths of the tree-rings in all samples were measured using WinDENDRO (Regent Instruments Inc (2015)), and the visual cross-dating results were statistically confirmed, using the COFECHA-software (Holmes, 1983). If the pith of the tree was missing (necessary for estimating the year of recruitment), we estimated the number of missing rings, using a pith locator (Speer, 2010).

The tree age at death (AAD) was calculated as the difference between the calendar year of the last ring, and the pith year. The years from death (YFD) was calculated as the difference between the sampling year (2015) and the cross-dated year of the last ring. In general, only trunks for which both variables could be calculated were included in the analyses, but to increase the sample size, we subjectively estimated these variables for six of the trees where the presence of bark could not be ascertained but only a small number of rings were missing. Age at death and years from death for each trunk are presented in Table A.1 in Supplementary data 1.

2.2.4. Dead wood data

2.2.4.1. Dead wood measurements. We collected a dead wood data to estimate the local dead wood continuity in the vicinity of each study trunk. Pieces of dead pine were recorded from four 10 m × 50 m transects, located in principal compass points around each study trunk. Transects to north and south begun at the trunk, and to west and east five meters from the trunk. If more than 10 m of a transect was unfeasible to locate due to the position of the trunk, two transects were established to the opposite principal compass point. Otherwise the unfeasible part (> 10 m) was turned 90° right. The transect was directed to a feasible half-cardinal point if it was not possible to establish a double transect to the opposite principal compass point.

We included all pieces of dead pine with a diameter of the wider end exceeding 10 cm, and fallen and standing dead wood with length or height ≥ 1 m. A piece of fallen dead wood was recorded only if its base was located inside the transect. The pieces were classified into categories of fallen and standing dead wood (including stumps formed by natural tree fall) and cut stumps. If the identification of tree species was uncertain due to the advanced decay stage, the piece was ignored.

For each piece of dead wood, the maximum diameter was measured. For standing and fallen dead wood, also the height (slant height measured with measuring tape if possible), minimum diameter and decay stage was recorded. A five-point decay stage estimation followed Renvall (1995).

2.2.4.2. Dead wood amount, diversity, and management intensity. Volumes were calculated for each recorded piece of fallen and standing dead wood, using the formula for truncated cone volume. We used the sum of volumes of standing and fallen dead wood in the four transects (total transect area was 1 ha) as the total dead wood volume ($m^3\,ha^{-1}$) on the site. The volumes of study trunks were added

Table 2
Site information, showing site level means and standard deviations (in brackets) for stand and trunk level variables (n for AAD and YFD indicated with upper index, for rest of the variables, n = 5 in all sites), and means for all sites. The units used for variables are in brackets. Column label abbreviations: DW = dead wood, stumps = management intensity, AAD = age at death, YFD = years from death, ø = diameter, canopy = canopy openness, dec./trunk = decomposer species richness, lic./trunk = *Micarea* species richness.

		Stand variables			Trunk variables					
	Site	DW div.	Stumps (pc ha^{-1})	DW amount (m^3 ha^{-1})	AAD (y)	YFD (y)	ø (cm)	Canopy (%)	Dec./trunk	Lic./trunk
1	Hallinmäki	2.0	94	13.4	130.8^4 (60.9)	25.8^4 (25.7)	17.0 (3.0)	12.2 (2.1)	3.2 (1.8)	1.4 (1.7)
2	Ilmakkamäki	2.3	40	25.2	108.7^3 (12.4)	19.0^3 (9.6)	33.4 (21.2)	15.6 (4.7)	3.0 (3.2)	1.8 (0.8)
3	Kalaja	1.8	30	5.7	147.0^2 (15.6)	12.0^2 (4.2)	31.3 (13.3)	16.8 (4.4)	3.6 (1.8)	3.2 (1.3)
4	Kirkkokangas	1.6	73	68.5	277.1^5 (42.5)	35.6^5 (9.8)	48.7 (9.5)	14.0 (2.7)	6.0 (1.7)	3.6 (1.9)
5	Kivetty	1.6	19	6.9	98.2^5 (10.4)	24.8^5 (7.9)	15.9 (3.7)	16.5 (2.6)	8.4 (1.1)	1.6 (1.5)
6	Kotinen	1.8	26	33.0	236.7^3 (30.6)	41.3^3 (17.9)	29.2 (9.4)	14.3 (3.8)	3.0 (1.2)	2.6 (2.5)
7	Kuusimäki	2.3	16	20.2	147.3^3 (16.6)	33.3^3 (11.7)	27.0 (10.1)	14.7 (1.1)	4.6 (1.1)	2.0 (1.2)
8	Latokuusikko	1.8	36	15.1	166.8^4 (28.6)	45.4^5 (8.2)	28.9 (6.7)	20.3 (5.1)	4.6 (2.4)	2.8 (1.3)
9	Leivonmäki	2.1	106	14.4	111.0^3 (13.5)	32.3^3 (10.3)	30.0 (9.8)	14.9 (3.8)	5.8 (3.1)	1.8 (0.8)
10	Lortikka	1.9	71	3.3	154.8^4 (67.0)	27.0^5 (13.6)	26.8 (5.8)	30.3 (17.2)	4.8 (1.6)	2.0 (2.0)
11	Pyhä-Häkki	2.5	22	61.6	293.3^3 (24.9)	43.3^4 (27.0)	33.4 (12.0)	23.1 (5.5)	6.0 (2.9)	1.6 (1.7)
12	Vaarunvuoret	1.6	112	2.8	144.0^4 (11.0)	31.8^4 (16.7)	24.4 (9.9)	11.8 (1.3)	4.8 (1.9)	2.6 (1.1)
13	Vesijako	2.4	38	25.4	147.0^5 (38.9)	29.8^5 (14.4)	33.7 (7.8)	12.6 (4.7)	5.2 (4.1)	2.8 (2.7)
14	Vuorilampi	2.2	69	22.3	82.8^4 (4.8)	29.0^4 (7.1)	23.8 (12.4)	11.2 (2.9)	5.2 (2.4)	4.0 (1.4)
	All sites	2.0 (0.3)	53.7 (32.3)	22.7 (19.5)	159.9^{52} (70.0)	31.5^{55} (15.3)	28.8 (12.3)	16.3 (7.3)	4.9 (2.5)	2.4 (1.7)

up to this estimate, calculated using the formula of right circular cone volume.

The stand continuity was described as diversity index for dead wood, calculated at the site level (Stokland, 2001). For the calculations, we constructed different dead wood types from the combinations of three variables: dead wood category (fallen/standing), canopy position (understory: ø < 30 cm; canopy: ø ≥ 30 cm), and decay stage (1–5). Altogether, there were 20 different dead wood types. The index used was Shannon's diversity index (H) (Shannon and Weaver, 1949):

$$H = -\sum_{i=1}^{s} p_i ln p_i$$

where p_i is the number of dead wood pieces in a certain dead wood type i (n) divided by the total amount of dead wood pieces (N), and s is the number of different dead wood types.

We used the number of cut stumps per hectare within a site as a measure of forest management intensity, calculated as the sum of stumps recorded from all the transects (sampled area was 1 ha).

2.3. Statistical methods

All analyses were conducted at trunk level separately for decomposers and *Micarea* lichens, and they were performed using R (version 3.3.2; R Core Team, 2016). Dead wood diversity and management intensity were the explanatory variables representing stand continuity, and age at death and years from death represented microhabitat continuity. Dead wood diversity was chosen instead of the dead wood amount as it presumably describes continuity better. Also, diameter and canopy openness were used to account for variation in survey effort and microclimate (Pouska et al., 2016b), respectively. Every explanatory variable was standardized to mean 0 ± 1 SE. Trunks with missing values in any of the measured variables were omitted from the analyses.

Before the analyses, correlations between explanatory variables were inspected. Tree diameter and age at death correlated strongly (Table A.2 in Supplementary data 1). Age at death was thought to be a more meaningful descriptor of microhabitat continuity of the trunks than diameter, and therefore it was chosen for the analyses of species richness.

A Generalized Linear Mixed Model (GLMM, n = 52) with a Poisson distribution and a log-linear link function was used to study which environmental variables best explained species richness of wood-inhabiting fungi (function "glmer" from the package "lme4" by Bates et al., 2016). Site and trunk identities were included into the models as hierarchically structured random effects by nesting the trunks within sites. The analysis was always started with a full model including all explanatory variables. Then, the model was simplified by removing the least significant variable from the model until only one variable remained. A model with the lowest AIC value was chosen.

We used Bioenv-analysis to study the effects of environmental variables on the community composition (function "bioenv" from the package "vegan" by Oksanen et al., 2017). First, we calculated binary Bray-Curtis dissimilarities for the pairs of communities from the presence-absence transformed species data. All species with only one occurrence and trunks with only one occurring species were excluded from the analyses. In the community data for decomposers, there were 36 species and 48 trunks, and for *Micarea* lichens, 12 species and 33 trunks. We performed Bioenv-analysis to find the best subset of environmental variables (calculated as Euclidean distances) having the highest Spearman rank correlation with the community dissimilarities. To visualize the effects of environmental variables on the community composition, we conducted Nonmetric Multidimensional Scaling (NMDS) with binary Bray-Curtis dissimilarities (function "metaMDS" from "vegan"). Finally, we chose the best two-dimensional solutions.

We also performed analyses on the responses of 14 individual species, namely those with high enough number of observations for reliable analyses. The methods considering these analyses, as well as their results are presented in Supplementary data 2.

3. Results

3.1. Species richness of wood-inhabiting fungi

Altogether, 107 fungal species were identified with a total of 510 occurrences (Table A.3 in Supplementary data 1). Out of these, 91 were decomposers and 16 *Micarea* lichens (the total number of detected species is somewhat higher than the number included in the analyses because we had to omit the communities for which some environmental variables could not be attained). The mean number of species per trunk was 4.9 for decomposers, and 2.4 for *Micarea* lichens (Table 2). 46% of the species (n = 49) occurred only once in the data. 21% (n = 23) of the species had over 5 occurrences, and 15% (n = 16) had over 10 occurrences. The 5 most common species were *Micarea melaena* (n = 45), *Glonium nitidum* (n = 33), *Micarea prasina* (n = 26), *Micarea misella* (n = 25), and Pyrenomycete sp. 4 (n = 23) (see Table A.3 in Supplementary data 1 for a full species list).

None of the variables entered into the GLMM model affected the decomposer species richness (Table 3), and canopy openness was the

Table 3
Results from GLMM analysis for species richness of decomposers and *Micarea* lichens (n = 52 for both datasets). Cells show estimates (B), standard errors (SE), z values, and statistical significances (P). Variables having a statistically significant effect are bolded. The units used for variables are in brackets. Abbreviations: canopy = canopy openness, YFD = years from death.

		B	SE	z value	P
Decomposers	(Intercept)	1.68	0.08	21.72	< 0.001
	Canopy (%)	0.08	0.08	1.05	0.295
Micarea lichens	(Intercept)	0.85	0.11	7.43	< 0.001
	YFD (y)	0.20	0.10	1.98	0.048

only variable remaining in the final model (Table 3; Fig. 2a). For *Micarea* lichens, species richness was positively dependent on years from death (Table 3; Fig. 2b). It was the only variable included in the final model (Table 3).

3.2. Community composition of wood-inhabiting fungi

The community composition of decomposers was best explained by dead wood diversity (Table 4; Fig. 3a). In NMDS, communities in the sites with the lowest dead wood diversities were located closer to each other in the center of the ordination space while communities in sites with higher dead wood diversities were more scattered (Fig. 3a). Years from death was the next fitted variable but it did not increase the correlation between the community dissimilarities and environmental distances (Table 4). Nevertheless, in NMDS communities on trunks with the least time since their death had mainly negative values on both axes (Fig. 3b). With increasing time since tree death, communities tended to be located closer to the upper right corner of the ordination space (Fig. 3b). The final stress level for the two-dimensional NMDS solution in Fig. 3a and b was 0.175.

The *Micarea* lichen community composition was most efficiently explained by the combined effect of years from death, site and dead wood diversity (Table 4; Fig. 3c and d). In NMDS, time since tree death increased towards the upper right corner of the ordination space (Fig. 3d), and dead wood diversity increased towards the lower right corner of the ordination space (Fig. 3c). However, as adding site increased the correlation between the community dissimilarities and environmental distances, the effect of years from death and dead wood diversity is not independent of site. The final stress level for the two-dimensional NMDS solution in Fig. 3c and 3d was 0.175. Altogether, the results for both decomposers and *Micarea* lichens should be interpreted with caution due to the low correlations in the Bioenv analyses.

In our analyses on the 14 individual species, four species were statistically significantly affected by some of the variables (Table B.1 in Supplementary data 2). Local continuity explained the presence of the species both positively and negatively. For the rest, the final models did not include any statistically significant variables. All results considering individual species are presented in Supplementary data 2.

Table 4
Results from Bioenv analyses of environmental variables affecting community composition of decomposers and *Micarea* lichens. Correlations are Spearman rank correlations between the community dissimilarities and environmental distances. Abbreviations: DW = dead wood, YFD = years from death, AAD = age at death, Stumps = management intensity, Canopy = canopy openness.

Decomposers

Size	Variables	Correlation
1	**DW diversity**	**0.128**
2	DW diversity, YFD	0.120
3	DW diversity, YFD, Site	0.109
4	DW diversity, YFD, Site, Diameter	0.099
5	DW diversity, YFD, Site, Diameter, AAD	0.078
6	DW diversity, YFD, Site, Diameter, AAD, Stumps	0.049
7	DW diversity, YFD, Site, Diameter, AAD, Stumps, Canopy	−0.011

Micarea lichens

Size	Variables	Correlation
1	YFD	0.126
2	YFD, Site	0.168
3	**YFD, Site, DW diversity**	**0.195**
4	YFD, Site, DW diversity, Stumps	0.177
5	YFD, Site, DW diversity, Stumps, AAD	0.160
6	YFD, Site, DW diversity, Stumps, AAD, Canopy	0.142
7	YFD, Site, DW diversity, Stumps, AAD, Canopy, Diameter	0.081

4. Discussion

4.1. Effects of stand continuity

Decomposers and *Micarea* lichens were affected by stand continuity through modest changes in the community composition that were driven by dead wood diversity. Communities of decomposers were more similar among sites with low dead wood diversity and differentiated when dead wood diversity increased. This might be because the communities in sites with low dead wood diversity might have more shared generalist species, able to survive in sites with more homogenous dead wood resources and thus, occurring more evenly across the landscapes (Nordén et al., 2013). With increasing dead wood diversity, sites can host more unique species assemblages including also specialists (Abrego and Salcedo, 2013; Nordén et al., 2013). Similar, although weaker trend occurred with *Micarea* lichens.

The species richness of decomposers or *Micarea* lichens was not affected by dead wood diversity or management intensity. Increased

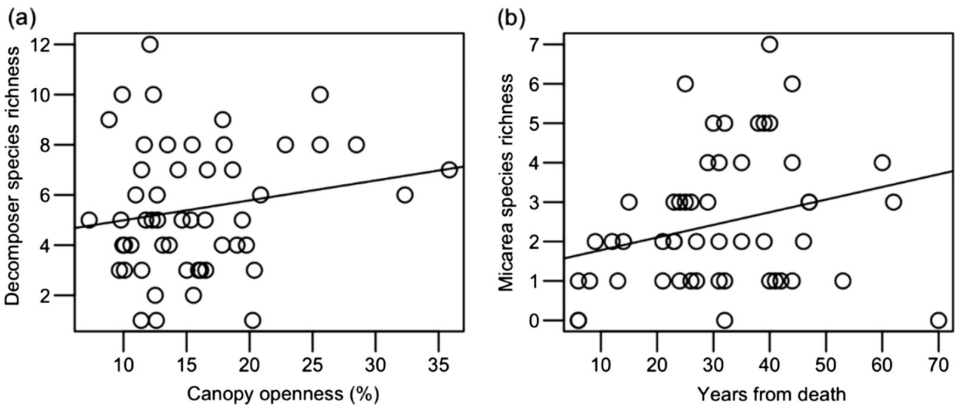

Fig. 2. Responses of (a) decomposer species richness to canopy openness and (b) *Micarea* species richness to the number of years from death. Each dot represents species richness on one trunk. Figures are presented only for variables included in the final models.

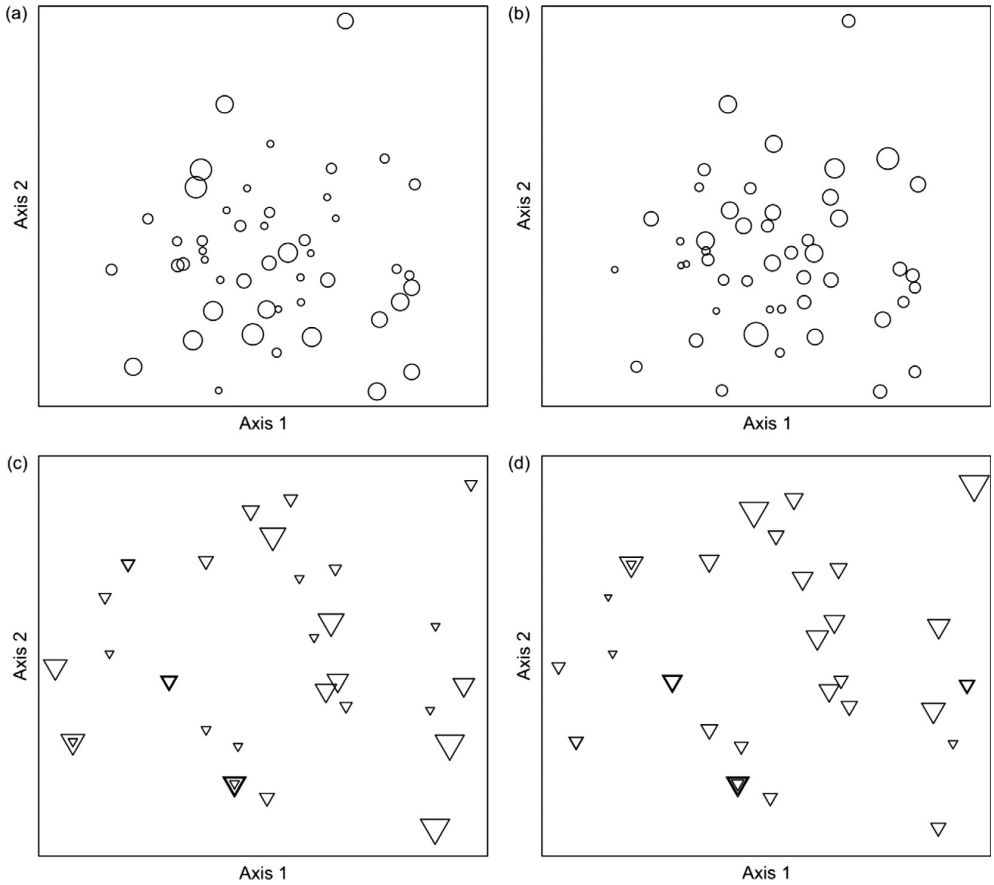

Fig. 3. NMDS representing the differences in community structure between the communities of decomposers (a and b; circles) and *Micarea* lichens (c and d; triangles) observed in the study. One symbol represents one community occurring on one trunk. The size of a symbol represents the magnitude of dead wood diversity in Fig. 3a and c, and the number of years from death in Fig. 3b and d. The size of a symbol grows with increasing values of the variables. Stress level for both solutions is 0.175.

dead wood diversity should contribute to a higher amount of available resources and niches (Siitonen, 2001; Stokland et al., 2012), and its positive effect on species richness of wood-inhabiting fungi has been demonstrated in previous studies (e.g., Hottola et al., 2009; Penttilä et al., 2004; Similä et al., 2006). Also, the negative effects of management intensity have been widely reported (e.g., Arnstadt et al., 2016; Bader et al., 1995).

In studies where all dead wood diversity (including also different tree species) has been measured to reflect the stand continuity, and the species richness has been measured from all of the material contributing to the dead wood diversity, it is very logical that clear positive correlations occur between species richness and stand continuity (see for example Hottola et al., 2009; Penttilä et al., 2004; Similä et al., 2006). Thus, it is worth emphasizing that as we measured only the dead wood diversity of pine, and recorded the fungal species richness only from the selected standing dead trees, such correlation might be more difficult to find. However, we argue that if such a correlation would be found it would truly reflect the species dependence on stand continuity, not just that more diverse substrate pool has more diverse species pool.

Species interactions might also play its part in the absence of a positive relationship between species richness and stand continuity. Heilmann-Clausen and Christensen (2005) found that the species richness of wood-inhabiting fungi on an individual tree was negatively affected by dead wood continuity (estimated as the proportion of strongly decayed logs). They suggested competitive exclusion to be one of the possible explanations: highly competitive specialists replace the early successional, non-specialist species in sites with high dead wood continuity. Thus, the species richness it not necessarily higher in the high continuity stands compared to stands with lower continuity, but can show no trends or even be lower.

In addition, the sites were located in or in the vicinity of conservation areas and thus, at least some natural forests were located in the proximity of sites. The variation in dead wood diversity and management intensity might not have been sufficient to reveal all existing trends. Moreover, management intensity of the sites was relatively low compared to the average managed forests in the area. In a study by Penttilä et al. (2004), dead wood diversity and management intensity induced a clear trend in polypore community composition when they compared communities in managed and old-growth forests. They recorded 400–500 stumps in managed stands, whereas the most managed site in this study included only 112 cut stumps per hectare.

The fact that stand continuity did not have a strong effect on decomposers and *Micarea* lichens gives indirect evidence that they are not dispersal limited at such fine spatial scales. In fact, it has been suggested that pine inhabiting fungi would be less affected by forest management than species specialized in e.g. spruce due to their better dispersal abilities (Stokland and Larsson, 2011). Stokland and Larsson (2011) hypothesized that this could be due to the different selection pressures in pine forests that experience forest fires and have lower input rates of dead wood than spruce forests. Thus, the sites may support viable metacommunities of these pine-inhabiting species if landscape level continuity is high. However, on rare specialist species, dispersal limitations might occur already at small spatial scales (Norros et al., 2012).

4.2. Effects of microhabitat continuity

Micarea species richness increased with time since tree death. Microhabitat continuity could be more important for *Micarea* lichens than stand continuity due to their slow rates of growth and establishment (Nordén et al., 2014; Stenroos et al., 2011). With increasing time since tree death there is more time available for colonization (Johansson et al., 2007), and new suitable microhabitats, such as decorticated wood appear (Renvall, 1995). The result also fits well with the hypothesis of species time relationship (Rosenzweig, 1995), especially because competitive exclusion has been suggested to be rare in lichens (Lawrey, 1991; Uliczka and Angelstam, 1999).

Species richness of decomposers was not affected by time since tree death. Previous studies have demonstrated an increase in species richness of wood-inhabiting fungi from initial decay stages to intermediate ones (Arnstadt et al., 2016; Renvall, 1995), and with time since tree death (Heilmann-Clausen, 2001). This pattern could result from changes in the tree quality (e.g. bark exfoliation (Renvall, 1995), and decreasing wood density in standing dead trees (Saint-Germain et al., 2007)), and from the emergence of late successional species (Høiland and Bendiksen, 1997). In the present study, the trunks with the longest time since their death probably included many kelo trees, i.e. standing dead trees characterized by slow death that makes the trunk very resistant to decay (Niemelä et al., 2002). Since kelos are utilized by a limited set of specialist species (Niemelä et al., 2002; Stokland et al., 2012), species richness might not increase linearly with time. Additionally, increasing competition with increasing habitat patch age might explain our result (Nordén and Appelqvist, 2001).

Community composition of both decomposers and *Micarea* lichens was slightly dependent on time since tree death. Communities on recently died trunks probably share certain (pioneer) species that inhabit the freshly dead wood (Niemelä et al., 1995; Renvall, 1995). Later on, fungal succession takes place with proceeding decomposition (Rajala et al., 2012; Stokland et al., 2012) and thus, different species of wood-inhabiting fungi should occur at different times after the tree death (Niemelä et al., 1995; Heilmann-Clausen, 2001). Trends in the community composition could have been stronger if more trunks at the end of the decomposition range could have been included in the analyses. The trunks for which the year of death could not be determined due to the erosion of the outermost tree rings were likely the oldest but had to be excluded from our analyses.

Tree age at death did not affect either of the studied fungal groups. This indicates that it might be important only for few species if any. The opposite was hypothesized as, for example, the community composition of dead wood might be affected by the longevity of infection history during the tree lifespan (Heilmann-Clausen and Christensen, 2004). Similar to the tree age at death, trunk diameter did not affect the communities of wood-inhabiting fungi. Several studies focusing on downed dead wood have reported the opposite (e.g., Høiland and Bendiksen, 1997; Renvall, 1995). However, our results are in accordance with the results by Pouska et al. (2016a) that showed no effect of diameter on wood-inhabiting fungal communities on standing dead Norway spruces. They suggested that diameter interacts with several other, more important trunk characteristics (e.g. trunk temperature and moisture) than diameter *per se.*

Also canopy openness did not affect wood-inhabiting fungal communities. Sun exposure may affect community composition of wood-inhabiting fungi (Heilmann-Clausen, 2001), and lichens have been shown to respond positively to increasing canopy openness (Marmor et al., 2012; Uliczka and Angelstam, 1999). Our results could be explained by milder edge effect in natural forest edges (Ruete et al., 2016) that were characteristic for our study sites. Moreover, canopy openness might be positively related to stand age, and thus light availability would not limit lichen communities in older stands (Bäcklund et al., 2016).

5. Conclusions

In the conservation areas of central Finland, wood-inhabiting fungal diversity was not significantly affected by local forest continuity. The results indicate that on a stand scale, other environmental filters and stochastic processes underlie the patterns of wood-inhabiting fungal diversity on standing dead pines. Although some species would depend on the continuous supply of dead wood and old trees, they seem not to be limited by dispersal, and can find these suitable habitats within the surrounding landscapes, underlining the importance of landscape level continuity.

The results demonstrated the importance of old, standing dead trees for species-rich communities of *Micarea* lichens. Conservation strategies concerning these species should aim to increase the local number of old trees that die and decay naturally. To achieve this, approaches of retention forestry should be applied in managed forests (Gustafsson et al., 2012; Lindenmayer et al., 2012). However, increasing the number of veteran trees in forest landscapes requires extending the time-frames of strategies that are currently applied in forest management (Lindenmayer et al., 2014).

The explicit relationship between local continuity and rare species remained unsolved. These species might be more sensitive to local continuity than common species when taking into consideration e.g. their highly specialized habitat use (Nordén et al., 2013). Therefore, rare and red-listed species should be at the center of future research on local continuity to be able to guide the required conservation actions, and to maintain these species also locally.

Acknowledgements

We would like to thank field assistants Meeri Väätäinen and Tapio Envall who helped with the data collection, Heikki Kotiranta who identified the difficult specimens of corticioid fungi, and Anna Oldén who provided statistical help. We are grateful to Dr. Fredericksen and an anonymous reviewer for constructive comments on an earlier version of the manuscript. The study was funded by the Ministry of the Environment (PUTTE grant to Halme and Leena Myllys), Societas Biologica Fennica Vanamo (grant to Saine), Societas pro Fauna et Fennica (grant to Saine), and the University of Helsinki Funds (grant to Aakala).

Appendix A. Supplementary material

Supplementary data (1–2) associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.11.045.

References

Abrego, N., Salcedo, I., 2013. Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: is it a question of quantity or quality? For. Ecol. Manage. 291, 377–385. http://dx.doi.org/10.1016/j.foreco.2012.11.025.

Abrego, N., Halme, P., Purhonen, J., Ovaskainen, O., 2016. Fruit body based inventories in wood-inhabiting fungi: should we replicate in space or time? Fungal Ecol. 20, 225–232. http://dx.doi.org/10.1016/j.funeco.2016.01.007.

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in north-western Europe. Ann. Bot.Fenn. 5, 169–211.

Arnstadt, T., Hoppe, B., Kahl, T., Kellner, H., Krüger, D., Bauhus, J., Hofrichter, M., 2016. Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. For. Ecol. Manage. 382, 129–142. http://dx.doi.org/10.1016/j.foreco.2016.10.004.

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. 72, 355–362. http://dx.doi.org/10.1016/0006-3207(94)00029-P.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Grothendieck, G., Green, P., 2016. lme4: Linear Mixed-Effects Model using 'Eigen' and S4, version 1.1-12. < https://cran.r-project.org/web/packages/lme4/lme4.pdf > (Accessed 30.11.2016).

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manage. 132, 39–50. http://dx.doi.org/10.1016/S0378-1127(00)00378-9.

Bäcklund, S., Jönsson, M., Strengbom, J., Frisch, A., Thor, G., 2016. A Pine is a Pine and a Spruce is a Spruce – the Effect of Tree Species and Stand Age on Epiphytic Lichen Communities. PLoS One 11, e0147004. http://dx.doi.org/10.1371/journal.pone.0147004.
Coppins, B.J., 1983. A taxonomic study of the lichen genus Micarea in Europe. Bull. Br. Museum Natural Hist Bot. 11, 1–204.
Czarnota, P., 2007. The lichen genus Micarea (Iecanorales, Ascomycota) in Poland. Polish Bot. Stud. 23, 1–197.
Czarnota, P., Guzow-Krzemínska, B., 2010. A phylogenetic study of the *Micarea prasina* group shows that *Micarea micrococca* includes three distinct lineages. Lichenol. 42, 7–21. http://dx.doi.org/10.1017/S0024282909990211.
Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. Ecol. Bull. 46, 16–47.
Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. E volution Syst. 34, 487–515. http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132419.
Flensted, K.K., Bruun, H.H., Ejrnæs, R., Eskildsen, A., Thomsen, P.F., Heilmann-Clausen, J., 2016. Red-listed species and forest continuity – a multi-taxon approach to conservation in temperate forests. For. Ecol. Manage. 378, 144–159. http://dx.doi.org/10.1016/j.foreco.2016.07.029.
Fritz, Ö., Gustafsson, L., Larsson, K., 2008. Does forest continuity matter in conservation? – a study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biol. Conserv. 141, 655–668. http://dx.doi.org/10.1016/j.biocon.2007.12.006.
Groven, R., Rolstad, J., Olaf, K., Rolstad, E., 2002. Using forest stand reconstructions to assess the role of structural continuity for late-successional species. For. Ecol. Manage. 164, 39–55. http://dx.doi.org/10.1016/S0378-1127(01)00611-9.
Gu, W., Heikkilä, R., Hanski, I., 2002. Esimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landsc. Ecol. 17, 699–710. http://dx.doi.org/10.1023/A:1022993317717.
Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. Bioscience 62, 633–645. http://dx.doi.org/10.1525/bio.2012.62.7.6.
Hanski, I., 2005. The Shrinking World: Ecological Consequences of Habitat Loss. In: Kinne, O. (Ed.), Excellence in Ecology, Book 14. International Ecology Institute, Oldendorf/Luhe, pp. 299.
Heilmann-Clausen, J., 2001. A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycol. Res. 105, 575–596. http://dx.doi.org/10.1017/S0953756201003665.
Heilmann-Clausen, J., Christensen, M., 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. For. Ecol. Manage. 201, 105–117. http://dx.doi.org/10.1016/j.foreco.2004.07.010.
Heilmann-Clausen, J., Christensen, M., 2005. Wood-inhabiting macrofungi in Danish beech-forests – conflicting diversity patterns and their implications in a conservation perspective. Biol. Conserv. 122, 633–642. http://dx.doi.org/10.1016/j.biocon.2004.10.001.
Herben, T., Rydin, H., Söderström, L., 1991. Spore establishment probability and the persistence of the fugitive invading moss, Orthodontium lineare: a spatial simulation model. Oikos 60, 215–221. http://dx.doi.org/10.2307/3544868.
Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull. 43, 69–78.
Hottola, J., Ovaskainen, O., Hanski, I., 2009. A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. J. Ecol. 97, 1320–1328. http://dx.doi.org/10.1111/j.1365-2745.2009.01583.x.
Høiland, K., Bendiksen, E., 1997. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sør-Trøndelag County, Central Norway. Nord. J. Bot. 16, 643–659. http://dx.doi.org/10.1111/j.1756-1051.1996.tb00283.x.
Johansson, P., Rydin, H., Thor, G., 2007. Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. Ecoscience 14, 81–91. http://dx.doi.org/10.2980/1195-6860(2007) 14[81:TARWEL]2.0.CO;2.
Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: a review. Biol. Conserv. 144, 11–20. http://dx.doi.org/10.1016/j.biocon.2010.07.010.
Krusic Jr., P.J., Hornbeck, J.W., 1989. Preserving decayed wood samples for tree-ring measurement. Tree-ring Bull. 49, 23–27.
Lawrey, J.D., 1991. Biotic interactions in lichen community development: a review. Lichenologist 23, 205–214. http://dx.doi.org/10.1017/S0024282991000373.
Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conserv. Lett. 5, 421–431. http://dx.doi.org/10.1111/j.1755-263X.2012.00257.x.
Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., Stein, J.A.R., 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. Conserv. Lett. 7, 61–69. http://dx.doi.org/10.1111/conl.12013.
Marmor, L., Törra, T., Saag, L., Randlane, T., 2012. Species richness of epiphytic lichens in coniferous forests: the effect of canopy openness. Ann. Bot. Fenn. 49, 352–358. http://dx.doi.org/10.5735/085.049.0606.
Natural Resources Institute Finland 2015. Monilähteinen valtakunnan metsien inventointi 2013, karttamuotoinen aineisto. http://kartta.metla.fi/ (Accessed 9.12.2016).
Niemelä, T., Wallenius, T., Kotiranta, H., 1995. Interactions of fungi at late stages of wood decomposition. Ann. Bot. Fenn. 32, 141–152.
Niemelä, T., Wallenius, T., Kotiranta, H., 2002. The kelo tree, a vanishing substrate of specified wood-inhabiting fungi. Polish Bot. J. 47, 91–101.
Nilsson, S., Baranowski, R., 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography 20, 491–498.
Nordén, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. Biodivers. Conserv. 10, 779–791. http://dx.doi.org/10.1023/A:1016675103935.
Nordén, B., Dahlberg, A., Brandrud, T.E., Fritz, Ö., Ejrnaes, R., Ovaskainen, O., 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. Ecoscience 21, 34–45. http://dx.doi.org/10.2980/21-1-3667.
Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J. Ecol. 101, 701–712. http://dx.doi.org/10.1111/1365-2745.12085.
Norros, V., Penttilä, R., Suominen, M., Ovaskainen, O., 2012. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. Oikos 121, 961–974. http://dx.doi.org/10.1111/j.1600-0706.2012.20052.x.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., McGlinn, P. R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. vegan: Community Ecology Package, version 2.4-4. < https://cran.r-project.org/web/packages/vegan/vegan.pdf > (Accessed 5.9.2017).
Paltto, H., Nordén, B., Götmark, F., Franc, N., 2006. At which spatial and temporal scales does landscape context affect local density of Red Data Book and Indicator species? Biol. Conserv. 133, 442–454. http://dx.doi.org/10.1016/j.biocon.2006.07.006.
Penttilä, R., Siitonen, J., Kuusinen, M., 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. Biol. Conserv. 117, 271–283. http://dx.doi.org/10.1016/j.biocon.2003.12.007.
Pouska, V., Macek, P., Zíbarová, L., 2016a. The relation of fungal communities to wood microclimate in a mountain spruce forest. Fungal Ecol. 21, 1–9. http://dx.doi.org/10.1016/j.funeco.2016.01.006.
Pouska, V., Macek, P., Zíbarová, L., Ostrow, H., 2016b. How does the richness of wood-decaying fungi relate to wood microclimate? Fungal Ecol. 1–4. http://dx.doi.org/10.1016/j.funeco.2016.06.006.
Purhonen, J., Huhtinen, S., Kotiranta, H., Kotiaho, J.S., Halme, P., 2016. Detailed information on fruiting phenology provides new insights on wood-inhabiting fungal detection. Fungal Ecol. 1–3. http://dx.doi.org/10.1016/j.funeco.2016.06.007.
Rajala, T., Peltoniemi, M., Pennanen, T., Mäkipää, R., 2012. Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests. FEMS Microbiol. Ecol. 81, 494–505. http://dx.doi.org/10.1111/j.1574-6941.2012.01376.x.
Ranius, T., Eliasson, P., Johansson, P., 2008. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. Biodivers. Conserv. 17, 2371–2381. http://dx.doi.org/10.1007/s10531-008-9387-3.
R Core Team. 2016. R: A language and environment for statistical computing. Version 3.3.2. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/ (Accessed 30.11. 2016).
Regent Instruments Inc. 2015 © 1995–2015. WinDENDRO software for annual tree-ring analysis. < http://www.regentinstruments.com/assets/windendro_about.html > (Accessed 26.11.2016).
Renvall, P., 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35, 1–51.
Riitters, K., Wickham, J., O'Neill, R., Jones, K.B., Smith, E., 2000. Global-scale patterns of forest fragmentation. Conserv. Ecol. 4 (2), 1–29.
Rolstad, J., Sætersdal, M., Gjerde, I., Storaunet, K.O., 2004. Wood-decaying fungi in boreal forest: are species richness and abundances influenced by small-scale spatio-temporal distribution of dead wood? Biol. Conserv. 117, 539–555. http://dx.doi.org/10.1016/j.biocon.2003.09.008.
Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.
Royal Botanic Gardens Kew, Landcare Research-NZ, Institute of Microbiology, Chinese Academy of Science, 2016. Index Fungorum. < http://www.indexfungorum.org/ > (Accessed 28.11.2016).
Ruete, A., Snäll, T., Jönsson, M., 2016. Dynamic anthropogenic edge effects on the distribution and diversity of fungi in fragmented old-growth forests. Ecol. Appl. 26, 1475–1485. http://dx.doi.org/10.1890/15-1271.
Saint-Germain, M., Drapeau, P., Buddle, C.M., 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography (Cop.) 30, 737–748. http://dx.doi.org/10.1111/j.2007.0906-7590.05080.x.
Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675. http://dx.doi.org/10.1038/nmeth.2089.
Shannon, C.D., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illimois Press, Urbana.
Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.
Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.L., Huhta, E., 2006. Co-variation and indicators of species diversity: can richness of forest-dwelling species be predicted in northern boreal forests? Ecol. Ind. 6, 686–700. http://dx.doi.org/10.1016/j.ecolind.2005.08.028.
Speer, J.H., 2010. Fundamentals of Tree-ring Research. The University of Arizona Press, Tuscon.
Stenroos, S., Ahti, T., Lohtander, K., Myllys, L., Haikonen, V. (Eds.), 2011. Suomen jäkäläopas. Kasvimuseo, Luonnontieteellinen keskusmuseo LUOMUS, Helsinki.
Stokland, J.N., 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecol. Bull. 49, 71–83.
Stokland, J., Kauserud, H., 2004. Phellinus nigrolimitatus – a wood-decomposing fungus highly influenced by forestry. For. Ecol. Manage. 187, 333–343. http://dx.doi.org/10.1016/j.foreco.2003.07.004.
Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge

University Press, Cambridge, UK.
Stokland, J., Larsson, K.-H., 2011. Legacies from natural forest dynamics: different effects of forest management on wood-inhabiting fungi in pine and spruce forests. For. Ecol. Manage. 261, 1707–1721. http://dx.doi.org/10.1016/j.foreco.2011.01.003.
Sverdrup-Thygeson, A., 2001. Can 'continuity indicator species' predict species richness or red-listed species of saproxylic beetles? Biodivers. Conserv. 10, 815–832.
Sverdrup-Thygeson, A., Lindenmayer, D.B., 2003. Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. For. Ecol. Manage. 174, 353–363. http://dx.doi.org/10.1016/S0378-1127(02)00043-9.
Tibell, L., 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forests. Nord. J. Bot. 12 (4), 427–450.
Tibell, L., 1999. Calicioid lichens and fungi. Nord. Lichen Flora 1, 20–94.
Uliczka, H., Angelstam, P., 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. Ecography (Cop.) 22, 396–405. http://dx.doi.org/10.1111/j.1600-0587.1999.tb00576.x.
Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as a monitoring tool for nature conservation. For. Ecol. Manage. 255, 1251–1261.
Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. 21, 414–416. http://dx.doi.org/10.1139/x91-053.

EFFECTS OF LOCAL FOREST CONTINUITY ON THE DIVERSITY OF FUNGI ON STANDING DEAD PINES

Saine Sonja, Aakala Tuomas, Purhonen Jenna, Launis Annina, Tuovila Hanna, Kosonen Timo & Halme Panu

Supplementary data 1. Supplementary tables (Tables A.1–A.3).

Table A.1. Study trunk information. The units used for variables are in brackets. AAD and YFD values with asterisks are rough estimations. Column label abbreviations: ø = diameter, AAD = age at death, YFD = years from death, Bark (%) = fraction of surface without bark cover, Lic. (%) = lichen coverage, Canopy (%) = canopy openness, Dec = species richness of decomposers, Lic = species richness of lichens, NA = data not available.

Site	Trunk ID	Height (m)	ø (cm)	AAD (y)	YFD (y)	Bark (%)	Lic. (%)	Decay stage	Canopy (%)	Species/trunk	
										Dec	Lic
Hallinmäki	1	3.7	14.6	NA	NA	92	88	4	11.7	3	1
	2	7.0	18.1	98	6	94	<1	2	12.7	5	0
	3	13.0	19.3	159	6	96	0	2	9.8	5	0
	4	9.0	13.1	65	60	81	92	2	11.4	1	4
	5	14.0	19.7	201	31	99	97	2	15.5	2	2
Ilmakkamäki	6	11.0	18.5	101	26	86	2	2	12.6	1	1
	7	7.5	13.4	102	23	64	9	2	10.6	4	2
	8	18.0	65.6	NA	NA	100	63	3	15.5	0	3
	9	3.8	43.0	NA	NA	95	87	3	16.4	2	2
	10	12.0	26.4	123	8	77	1	2	22.8	8	1
Kalaja	11	14.0	27.4	136	9	65	<1	2	12.7	6	2
	12	1.4	51.6	NA	NA	99	98	4	23.0	1	5
	13	12.0	28.3	NA	NA	82	72	2	12.5	4	2
	14	1.9	15.0	158	15	29	3	3	17.8	4	3
	15	3.1	34.1	NA	NA	99	84	4	18.0	3	4
Kivetty	16	8.5	15.6	95	27	82	1	2	18.0	8	1
	17	6.2	10.5	97	32	33	37	2	18.7	7	0
	18	7.0	19.4	108	13	94	38	2	17.9	9	1
	19	7.5	19.1	83	31	32	84	2	12.4	10	4
	20	6.5	14.6	108	21	79	27	2	15.4	8	2
Kirkkokangas	21	17.0	57.9	243.5*	44	90	23	3	11.4	7	6
	22	22.0	43.3	314	26	97	9	3	14.3	7	3
	23	20.0	60.2	313.2*	24	83	10	2	11.0	6	3
	24	14.0	40.7	221*	40*	82	99	2	16.7	7	5
	25	15.0	41.4	294	44	78	1	2	16.5	3	1
Kotinen	26	12.0	21.3	202	62	99	92	3	12.5	2	3
	27	3.5	45.2	NA	NA	95	62	4	12.1	3	0
	28	9.0	23.6	NA	NA	94	88	3	11.0	2	0
	29	14.0	29.0	260	30	92	73	3	20.4	3	5
	30	3.7	27.1	248	32	94	95	4	15.3	5	5
Kuusimäki	31	23.0	23.9	132	31	94	21	2	13.1	4	1
	32	12.0	14.3	NA	NA	100	97	3	14.3	5	4
	33	18.0	41.7	165	23	22	12	2	15.9	3	2
	34	23.0	30.4	145	46	64	4	2	14.6	5	2
	35	2.3	24.5	NA	NA	100	72	4	15.6	6	1
Latokuusikko	36	31.0	36.6	144	47	40	1	2	28.5	8	3
	37	27.0	19.1	141	35	53	8	2	19.8	4	4
	38	22.0	25.6	198	39	7	92	2	20.9	6	2
	39	25.0	31.5	184	53	95	60	2	15.0	3	1
	40	18.0	31.5	NA	53	72	2	2	17.3	2	4
Leivonmäki	41	1.3	44.2	NA	NA	100	95	3	17.8	3	2
	42	13.0	22.3	122	21	92	1	2	19.4	5	1
	43	11.0	23.1	115	35	35	57	2	13.5	8	2
	44	13.0	24.2	96	41	25	27	2	9.9	10	1
	45	2.3	36.3	NA	NA	99	87	3	13.7	3	3

(*continued on the next page*)

Lortikka	46	2.0	34.1	98	25	68	4	3	35.9	7	3
	47	14.0	19.7	250	40	77	78	2	32.3	6	1
	48	2.8	28.5	NA	26	83	87	3	54.6	4	1
	49	24.0	29.6	150	38	70	NA	3	19.0	4	5
	50	15.0	22.3	121	6	100	NA	2	9.7	3	0
Pyhä-Häkki	51	17.0	29.9	302.9*	27	92	36	2	16.5	5	2
	52	15.0	22.0	265	70	97	42	2	25.6	10	0
	53	16.0	24.2	NA	NA	38	4	2	18.3	4	0
	54	18.0	40.4	312	14	86	28	3	25.6	8	2
	55	6.0	50.6	NA	62	96	47	3	29.6	3	4
Vaarunvuoret	56	14.0	31.2	148*	44*	87	90	2	12.3	5	4
	57	7.5	9.9	NA	NA	26	8	2	11.5	4	3
	58	12.0	22.3	156	24	46	37	2	10.1	3	1
	59	18.0	35.8	130	47	92	73	2	11.7	8	3
	60	6.0	22.9	142	12	42	11	2	13.6	4	2
Vesijako	61	12.0	29.9	99	32	87	4	2	11.8	5	1
	62	12.0	32.5	140	29	58	34	2	12.1	12	4
	63	16.0	36.9	183.7*	6	93	0	2	7.3	5	1
	64	16.0	44.9	189	42	93	87	3	20.3	1	1
	65	18.0	24.2	123	40	97	98	2	11.5	3	7
Vuorilampi	66	1.1	44.6	NA	NA	98	94	4	11.1	6	3
	67	14.0	20.1	77	39	96	83	3	8.9	9	5
	68	8.6	13.7	88	25	92	86	2	16.1	3	6
	69	16.0	24.5	81	23	38	25	2	10.1	4	3
	70	10.0	15.9	85	29	97	43	2	10.0	4	3

Table A.2. Correlations between variables used in the analyses (n_{AAD} = 52, n_{YFD} = 55, for all others n = 70). Cells show Spearman rank correlation coefficients, except for cells with superscript P showing Pearson's correlation coefficient. Correlations > 0.20 are bolded. Decomposers/trunk and lichens/trunk indicate the species richness of the studied fungal groups. Dead wood (DW) diversity was calculated with Shannon's diversity index. The units used for variables are in brackets. Abbreviations: DW = dead wood, stumps = management intensity, ø = diameter, AAD = age at death, YFD = years from death, canopy = canopy openness.

	DW diversity	Stumps (pc ha^{-1})	ø (cm)	AAD (y)	YFD (y)	Canopy (%)
Stumps (pc ha^{-1})	**-0.25**	1				
ø (cm)	0.06	0.03	1			
AAD (y)	-0.14	-0.05	**0.62**^{P}	1		
YFD (y)	-0.04	-0.05	0.18^{P}	0.14^{P}	1	
Canopy (%)	0.06	**-0.32**	0.16^{P}	**0.30**^{P}	0.19^{P}	1
Decomposers/trunk	-0.10	-0.08	-0.09	-0.10	-0.09	0.05
Lichens/trunk	-0.16	0.07	0.19	0.02	**0.33**	-0.01

Table A.3. Fungal species observed in the study (n = 107). Species nomenclature follows Coppins (1983), Czarnota (2007), and Czarnota and Guzow-Krzemínska (2010) with *Micarea* species, Tibell (1999) with mycocalicioid species, and Index Fungorum with the rest (Royal Botanic Gardens Kew et al., 2016). Conservation statuses are in brackets after a species name. Statuses follow the 2010 Red List of Finnish Species (Rassi et al., 2010): NE = not evaluated, LC = least concerned, NT = near threatened, and VU = vulnerable (IUCN, 2012). Species marked with asterisks had not been detected in Finland by the latest evaluation of threatened species in 2010. Statuses were derived from Rassi et al. (2010), Finnish Biodiversity Info Facility (2017) and unpublished information received from the Finnish Expert Group of Fungi. Statuses were not given for species with tentative names. Genus *Chaenothecopsis* and species *C. nana, C. savonica, Micarea micrococca* and *Mycocalicium subtile* have been divided into multiple species new to science. Working titles are marked with quotation marks. n is the number of study trunks on which the species occurred on, and % is the proportion these trunks represent out of all trunks (n = 70). Cells show means and standard deviations (in brackets) for environmental variables, separately for the trunks on which the species was found to be present (1) or absent (0). For AAD, N = 52, for YFD, N = 55, and for the rest, N = 70. Means for AAD and YFD marked with superscript § do not represent the mean for full n of occurrences (or absences), since the calculations also include trunks for which the data was not available. NA (data not available) indicates that data was not available for any of the trunks species occurred on. The units used for variables are in brackets. Dead wood (DW) diversity was calculated with Shannon's diversity index. Column label abbreviations: stumps = management intensity, ø = diameter, AAD = age at death, YFD = years from death, canopy = canopy openness. Taxonomic abbreviations: agg. = species aggregate, cf. = uncertain determination, coll. = in a collective sense, sp. = species, sp. nov. = species being introduced for the first time (Knudsen and Vesterholt, 2008).

			DW diversity		Stumps (pc ha^{-1})		ø (cm)		AAD (y)		YFD (y)		Canopy (%)	
Species	n	%	1	0	1	0	1	0	1	0	1	0	1	0
*Actidium hysterioides**	15	21.4	1.8 (0.2)	2.0 (0.3)	54.3 (30.1)	53.6 (33.1)	26.4 (12.3)	29.5 (12.3)	163.2 (73.0)	158.5§ (69.7)	23.3 (13.4)	34.6§ (14.9)	16.6 (7.0)	16.2 (7.4)
Amyloporia sinuosa (LC)	1	1.4	1.8 (0.0)	2.0 (0.3)	26.0 (0.0)	54.1 (32.3)	27.1 (0.0)	28.8 (12.4)	248.0 (0.0)	158.1§ (69.6)	32.0 (0.0)	31.5§ (15.4)	15.4 (0.0)	16.3 (7.3)
Aphanobasidium pseudotsugae (LC)	1	1.4	2.2 (0.0)	2.0 (0.3)	69.0 (0.0)	53.5 (32.5)	20.1 (0.0)	28.9 (12.3)	77.0 (0.0)	161.5§ (69.7)	39.0 (0.0)	31.4§ (15.4)	8.9 (0.0)	16.4 (7.3)
Ascocoryne sp. 1	1	1.4	2.2 (0.0)	2.0 (0.3)	69.0 (0.0)	53.5 (32.5)	15.9 (0.0)	29.0 (12.3)	85.0 (0.0)	161.3§ (69.9)	29.0 (0.0)	31.6§ (15.4)	10.0 (0.0)	16.4 (7.3)
Athelia decipiens (LC)	1	1.4	1.8 (0.0)	2.0 (0.3)	36.0 (0.0)	53.0 (32.4)	36.6 (0.0)	28.7 (12.3)	144.0 (0.0)	160.2§ (70.6)	47.0 (0.0)	31.2§ (15.3)	28.5 (0.0)	16.1 (7.2)
Athelia sp. 1	1	1.4	1.6 (0.0)	2.0 (0.3)	19.0 (0.0)	54.2 (32.2)	15.6 (0.0)	29.0 (12.3)	95.0 (0.0)	161.1§ (70.1)	27.0 (0.0)	31.6§ (15.4)	18.0 (0.0)	16.3 (7.3)
Botryobasidium subcoronatum (LC)	1	1.4	2.3 (0.0)	2.0 (0.3)	16.0 (0.0)	54.3 (32.2)	23.9 (0.0)	28.9 (12.3)	132.0 (0.0)	160.4§ (70.6)	31.0 (0.0)	31.5§ (15.4)	13.1 (0.0)	16.4 (7.3)

(*continued on the next page*)

Species	n	%	DW diversity		Stumps (pc ha^{-1})		ø (cm)		AAD (y)		YFD (y)		Canopy (%)	
			1	0	1	0	1	0	1	0	1	0	1	0
Botryobasidium vagum (LC)	4	5.7	2.3 (0.2)	2.0 (0.3)	49.5 (23.4)	54.0 (32.9)	22.0 (7.8)	29.2 (12.4)	142.5 (86.2)	161.3§ (69.4)	40.8 (20.4)	30.8§ (14.8)	12.6 (5.4)	16.5 (7.3)
Capronia sp. 1	2	2.9	2.2 (0.1)	2.0 (0.3)	42.5 (37.5)	54.0 (32.4)	23.2 (10.2)	29.0 (12.4)	115.0 (42.4)	161.7§ (70.5)	37.5 (12.0)	31.3§ (15.4)	12.3 (3.3)	16.4 (7.3)
Ceraceomyces microsporus (LC)	3	4.2	1.9 (0.34)	2.0 (0.3)	29.7 (10.5)	54.8 (32.5)	22.7 (9.9)	29.1 (12.4)	98.0§ (4.2)	162.3§ (70.3)	26.5§ (0.7)	31.7§ (15.5)	16.2 (3.1)	16.3 (7.4)
Chaenothecopsis 1 "green"	3	4.2	2.1 (0.2)	2.0 (0.3)	52.7 (47.3)	53.8 (32.0)	33.4 (10.0)	28.6 (12.4)	184.0§ (0.0)	159.4§ (70.6)	53.0§ (0.0)	31.1§ (15.1)	16.1 (1.4)	16.3 (7.4)
Chaenothecopsis 2	1	1.4	2.3 (0.0)	2.0 (0.3)	16.0 (0.0)	54.3 (32.2)	30.4 (0.0)	28.8 (12.4)	145.0 (0.0)	160.1§ (70.7)	46.0 (0.0)	31.3§ (15.3)	14.7 (0.0)	16.3 (7.3)
Chaenothecopsis 3	1	1.4	2.1 (0.0)	2.0 (0.3)	106.0 (0.0)	53.0 (31.9)	24.2 (0.0)	28.9 (12.3)	96.0 (0.0)	161.1§ (70.1)	41.0 (0.0)	31.4§ (15.4)	9.9 (0.0)	16.4 (7.3)
Chaenothecopsis 4 "håkon"	1	1.4	1.7 (0.0)	2.0 (0.3)	26.0 (0.0)	54.1 (32.3)	45.2 (0.0)	28.6 (12.2)	NA	159.9§ (70.0)	NA	31.5§ (15.3)	12.1 (0.0)	16.4 (7.3)
Chaenothecopsis 5	2	2.9	1.8 (0.3)	2.0 (0.3)	109.0 (4.2)	52.1 (31.3)	27.1 (24.3)	28.9 (12.1)	NA	159.9§ (70.0)	NA	31.5§ (15.3)	14.6 (4.4)	16.4 (7.3)
Chaenothecopsis 6 "sturdy"	2	2.9	1.7 (0.1)	2.0 (0.3)	69.0 (60.8)	53.3 (31.8)	32.4 (4.8)	28.7 (12.4)	195.0 (91.9)	158.5§ (69.8)	38.5 (12.0)	31.3§ (15.4)	16.0 (6.2)	16.3 (7.3)
Chaenothecopsis 7	1	1.4	1.6 (0.0)	2.0 (0.3)	112.0 (0.0)	52.9 (31.7)	35.8 (0.0)	28.7 (12.3)	130.0 (0.0)	160.4§ (70.6)	47.0 (0.0)	31.2§ (15.3)	11.7 (0.0)	16.4 (7.3)
Chaenothecopsis 8	1	1.4	2.5 (0.0)	2.0 (0.3)	22.0 (0.0)	54.2 (32.3)	40.4 (0.0)	28.6 (12.3)	312.0 (0.0)	156.9§ (67.3)	14.0 (0.0)	31.9§ (15.2)	29.6 (0.0)	16.1 (7.1)
Chaenothecopsis 9	2	2.9	1.6 (0.0)	2.0 (0.3)	112.0 (0.0)	52.0 (31.1)	33.5 (3.3)	28.7 (12.4)	139.0 (12.7)	160.7§ (71.2)	45.5 (2.1)	31.0§ (15.3)	12.0 (0.4)	16.4 (7.3)
Chaenothecopsis consociata (LC)	1	1.4	1.8 (0.0)	2.0 (0.3)	26.0 (0.0)	54.1 (32.3)	23.6 (0.0)	28.9 (12.3)	NA	159.9§ (70.0)	NA	31.5§ (15.3)	11.1 (0.0)	16.4 (7.3)
Chaenothecopsis nana "grey"	3	4.2	2.2 (0.5)	2.0 (0.3)	21.0 (1.7)	55.2 (32.2)	23.8 (5.5)	29.0 (12.5)	225.3 (103.3)	155.9§ (66.9)	36.7 (29.7)	31.2§ (14.5)	17.6 (1.0)	16.2 (7.4)
Chaenothecopsis nana "thin"	1	1.4	2.3 (0.0)	2.0 (0.3)	40.0 (0.0)	53.9 (32.5)	26.4 (0.0)	28.8 (12.4)	123.0 (0.0)	160.6§ (70.5)	8.0 (0.0)	32.0§ (15.1)	22.8 (0.0)	16.2 (7.3)
Chaenothecopsis pusiola (LC)	22	31.4	1.9 (0.3)	2.0 (0.3)	54.4 (32.8)	53.4 (32.4)	27.1 (9.1)	29.6 (13.5)	143.4§ (58.8)	169.3§ (74.9)	37.1§ (11.5)	28.1§ (16.4)	17.3 (10.5)	15.8 (5.3)
Chaenothecopsis savonica "conifer"	6	8.6	2.1 (0.3)	2.0 (0.3)	60.2 (28.1)	53.1 (32.8)	27.7 (8.1)	28.9 (12.6)	159.8§ (65.0)	159.9§ (71.0)	33.0§ (6.2)	31.4§ (15.9)	19.8 (17.5)	16.0 (5.7)

(*continued on the next page*)

Species	n	%	DW diversity		Stumps (pc ha^{-1})		ø (cm)		AAD (y)		YFD (y)		Canopy (%)	
			1	0	1	0	1	0	1	0	1	0	1	0
Chaenothecopsis savonica "wide-spored"	4	5.7	1.9 (0.3)	2.0 (0.3)	67.5 (39.4)	52.9 (32.0)	22.4 (9.7)	29.2 (12.4)	181.7§ (59.2)	158.5§ (70.9)	41.3§ (4.2)	31.0§ (15.5)	19.4 (9.2)	16.1 (7.2)
Chaenothecopsis savonica "roundheaded"	2	2.9	2.1 (0.1)	2.0 (0.3)	81.5 (17.7)	52.9 (32.3)	15.3 (0.9)	29.2 (12.2)	85.0§ (0.0)	161.3§ (69.9)	29.0§ (0.0)	31.6§ (15.4)	10.8 (1.3)	16.5 (7.3)
Chaenothecopsis savonica "long-spored"	2	2.9	2.1 (0.4)	2.0 (0.3)	54.5 (23.3)	53.7 (32.6)	33.3 (1.1)	28.7 (12.4)	119.0 (29.7)	161.5§ (70.8)	27.0 (2.8)	31.7§ (15.5)	21.6 (20.2)	16.2 (6.9)
Chaenothecopsis savonica "sturdy"	1	1.4	1.8 (0.0)	2.0 (0.3)	36.0 (0.0)	54.0 (32.4)	19.1 (0.0)	29.0 (12.3)	141.0 (0.0)	160.2§ (70.6)	35.0 (0.0)	31.5§ (15.4)	19.8 (0.0)	16.3 (7.3)
Chaenothecopsis savonica "wine"	4	5.7	1.9 (0.3)	2.0 (0.3)	80.3 (17.3)	52.1 (32.3)	45.4 (10.4)	27.8 (11.7)	267.1§ (65.2)	155.6§ (67.3)	32.0§ (11.3)	31.5§ (15.5)	13.1 (2.7)	16.5 (7.4)
Chaenothecopsis viridireagens (LC)	11	15.7	1.9 (0.3)	2.0 (0.3)	56.0 (26.8)	53.3 (33.4)	36.2 (16.1)	27.4 (11.1)	193.8§ (87.8)	155.4§ (67.2)	40.9§ (16.2)	30.2§ (14.8)	16.3 (7.9)	16.3 (7.2)
Claussenomyces atrovirens (NE)	2	2.9	1.9 (0.3)	2.0 (0.3)	62.5 (61.5)	53.5 (31.8)	21.1 (2.8)	29.0 (12.4)	99.0 (22.6)	162.3§ (70.2)	33.0 (2.8)	31.5§ (15.5)	12.9 (0.8)	16.4 (7.3)
Collybia cirrhata (LC)	1	1.4	1.6 (0.0)	2.0 (0.3)	112.0 (0.0)	52.9 (31.7)	31.2 (0.0)	28.8 (12.4)	148.0 (0.0)	160.1§ (70.7)	44.0 (0.0)	31.3§ (15.3)	12.3 (0.0)	16.4 (7.3)
Coniochaeta ligniaria (LC)	2	2.9	2.3 (0.0)	2.0 (0.3)	40.0 (0.0)	54.1 (32.7)	19.9 (9.2)	29.1 (12.3)	112.5 (14.9)	161.8§ (70.7)	15.5 (10.6)	32.1§ (15.2)	16.7 (8.7)	16.3 (7.3)
Coniophora olivacea (LC)	1	1.4	2.5 (0.0)	2.0 (0.3)	22.0 (0.0)	54.2 (32.3)	40.4 (0.0)	28.6 (12.3)	312.0 (0.0)	156.9§ (67.3)	14.0 (0.0)	31.9§ (15.2)	29.6 (0.0)	16.1 (7.1)
Coniophora puteana (LC)	1	1.4	1.8 (0.0)	2.0 (0.3)	30.0 (0.0)	54.1 (32.4)	27.4 (0.0)	28.8 (12.4)	136.0 (0.0)	160.3§ (70.6)	9.0 (0.0)	31.9§ (15.1)	12.7 (0.0)	16.4 (7.3)
Crumenulopsis pinicola (NE)	1	1.4	1.8 (0.0)	2.0 (0.3)	30.0 (0.0)	54.1 (32.4)	27.4 (0.0)	28.8 (12.4)	136.0 (0.0)	160.3§ (70.6)	9.0 (0.0)	31.9§ (15.1)	12.7 (0.0)	16.4 (7.3)
*Cryptodiscus pini**	2	2.9	2.2 (0.1)	2.0 (0.3)	42.5 (37.5)	54.1 (32.4)	17.2 (4.1)	29.2 (12.3)	77.0§ (0.0)	161.5§ (69.7)	39.0§ (0.0)	31.4§ (15.4)	11.6 (3.8)	16.4 (7.3)
Dacrymyces lacrymalis (LC)	1	1.4	2.0 (0.0)	2.0 (0.3)	94.0 (0.0)	53.1 (32.1)	19.7 (0.0)	28.9 (12.3)	201.0 (0.0)	159.1§ (70.4)	31.0 (0.0)	31.5§ (15.4)	15.6 (0.0)	16.3 (7.3)
Dacrymyces microsporus (LC)	1	1.4	2.4 (0.0)	2.0 (0.3)	38.0 (0.0)	53.9 (32.5)	44.9 (0.0)	28.6 (12.2)	189.0 (0.0)	159.3§ (70.6)	42.0 (0.0)	31.3§ (15.3)	11.5 (0.0)	16.4 (7.3)
Dacrymyces stillatus (LC)	6	8.6	2.0 (0.4)	2.0 (0.3)	43.3 (22.3)	54.7 (33.0)	42.8 (10.5)	27.5 (11.6)	308.0§ (7.3)	153.9§ (64.5)	25.5§ (2.1)	31.8§ (15.5)	14.2 (3.2)	16.5 (7.5)
Dacrymyces tortus (LC)	6	8.6	2.1 (0.4)	2.0 (0.3)	24.5 (7.7)	56.5 (32.4)	27.3 (8.5)	29.0 (12.6)	198.8§ (99.1)	156.6§ (67.4)	25.5§ (7.9)	32.0§ (15.6)	16.1 (7.6)	16.3 (7.3)

(*continued on the next page*)

Species	n	%	DW diversity		Stumps (pc ha^{-1})		ø (cm)		AAD (y)		YFD (y)		Canopy (%)	
			1	0	1	0	1	0	1	0	1	0	1	0
Dermateaceae sp. 1	1	1.4	2.1 (0.0)	2.0 (0.3)	106.0 (0.0)	53.0 (31.9)	23.1 (0.0)	28.9 (12.3)	115.0 (0.0)	160.7§ (70.4)	35.0 (0.0)	31.5§ (15.4)	13.5 (0.0)	16.3 (7.3)
Exidia saccharina (LC)	1	1.4	2.0 (0.0)	2.0 (0.3)	94.0 (0.0)	53.1 (32.1)	19.3 (0.0)	29.0 (12.3)	159.0 (0.0)	159.9§ (70.7)	6.0 (0.0)	32.0§ (15.0)	9.8 (0.0)	16.4 (7.3)
Fomitopsis pinicola (LC)	7	10.0	2.1 (0.3)	2.0 (0.3)	38.3 (23.3)	55.4 (32.8)	29.5 (10.3)	28.7 (12.5)	194.2§ (76.1)	155.4§ (68.8)	28.7 (22.4)	31.9§ (14.2)	24.9 (14.8)	15.3 (5.3)
Galerina marginata (LC)	1	1.4	1.8 (0.0)	2.0 (0.3)	26.0 (0.0)	54.1 (32.3)	27.1 (0.0)	28.8 (12.4)	248.0 (0.0)	158.1§ (69.6)	32.0 (0.0)	31.5§ (15.4)	15.4 (0.0)	16.3 (7.3)
Galerina sp. 1	1	1.4	1.6 (0.0)	2.0 (0.3)	73.0 (0.0)	53.4 (32.4)	40.7 (0.0)	28.6 (12.3)	221.0 (0.0)	158.7§ (70.1)	40.0 (0.0)	31.4§ (15.4)	16.7 (0.0)	16.3 (7.3)
Galerina stylifera (LC)	1	1.4	2.3 (0.0)	2.0 (0.3)	16.0 (0.0)	54.3 (32.2)	14.3 (0.0)	29.0 (12.2)	NA	159.9§ (70.0)	NA	31.5§ (15.3)	14.3 (0.0)	16.3 (7.3)
Globulicium hiemale (LC)	2	2.9	2.0 (0.4)	2.0 (0.3)	21.0 (7.1)	54.7 (32.2)	29.8 (21.8)	28.8 (12.2)	NA	159.9§ (70.0)	NA	31.5§ (15.3)	13.2 (1.5)	16.4 (7.3)
*Glonium nitidum**	33	47.1	1.9 (0.3)	2.0 (0.3)	54.5 (34.5)	53.1 (30.6)	28.9 (10.8)	28.7 (13.6)	166.2§ (77.4)	152.4§ (61.1)	29.0§ (15.3)	34.6§ (14.9)	17.5 (6.9)	15.2 (7.5)
Gymnopilus penetrans (LC)	2	2.9	1.8 (0.2)	2.0 (0.3)	45.0 (36.8)	54.0 (32.4)	24.4 (7.4)	28.9 (12.4)	116.5 (47.4)	161.6§ (70.5)	34.5 (5.0)	31.4§ (15.5)	15.7 (4.7)	16.3 (7.3)
Gymnopus androsaceus (LC)	5	7.1	2.1 (0.3)	2.0 (0.3)	44.2 (36.4)	54.5 (32.1)	21.2 (5.1)	29.4 (12.5)	111.0 (19.1)	165.1§ (71.5)	25.6 (10.8)	32.1§ (15.6)	14.5 (4.8)	16.4 (7.4)
Hastodontia hastata (LC)	1	1.4	2.2 (0.0)	2.0 (0.3)	69.0 (0.0)	53.5 (32.5)	44.6 (0.0)	28.6 (12.2)	NA	159.9§ (70.0)	NA	31.5§ (15.3)	11.1 (0.0)	16.4 (7.3)
Hyalorbilia sp. 1	1	1.4	1.8 (0.0)	2.0 (0.3)	36.0 (0.0)	54.0 (32.4)	36.6 (0.0)	28.7 (12.3)	144.0 (0.0)	160.2§ (70.6)	47.0 (0.0)	31.2§ (15.3)	28.5 (0.0)	16.1 (7.2)
Hyaloscypha aureliella (LC)	1	1.4	1.6 (0.0)	2.0 (0.3)	19.0 (0.0)	54.2 (32.2)	19.4 (0.0)	28.9 (12.3)	108.0 (0.0)	160.9§ (70.3)	13.0 (0.0)	31.9§ (15.2)	17.9 (0.0)	16.3 (7.3)
Hyphodontia abieticola (LC)	2	2.9	1.8 (0.3)	2.0 (0.3)	83.5 (14.9)	52.8 (32.3)	35.5 (31.7)	28.6 (11.8)	154.2 (126.2)	160.1§ (69.1)	52.0 (11.3)	30.8§ (14.9)	11.4 (0.0)	16.4 (7.3)
Hypochnicium cf. *punctulatum* (LC)	1	1.4	2.3 (0.0)	2.0 (0.3)	16.0 (0.0)	54.3 (32.2)	41.7 (0.0)	28.6 (12.3)	165.0 (0.0)	159.8§ (70.7)	23.0 (0.0)	31.7§ (15.4)	16.0 (0.0)	16.3 (7.3)
*Hypochnicium cremicolor**	1	1.4	1.6 (0.0)	2.0 (0.3)	73.0 (0.0)	53.4 (32.4)	43.3 (0.0)	28.6 (12.2)	314.0 (0.0)	156.8§ (67.2)	26.0 (0.0)	31.6§ (15.4)	14.3 (0.0)	16.3 (7.3)
Lophium mytilinum (LC)	6	8.6	2.0 (0.4)	2.0 (0.3)	43.5 (23.5)	54.7 (33.0)	28.1 (15.2)	28.9 (12.1)	176.4 (68.4)	157.7§ (70.6)	31.3 (24.5)	31.6§ (14.1)	16.4 (5.2)	16.3 (7.5)

(*continued on the next page*)

Species	n	%	DW diversity		Stumps (pc ha^{-1})		ø (cm)		AAD (y)		YFD (y)		Canopy (%)	
			1	0	1	0	1	0	1	0	1	0	1	0
Micarea anterior (VU)	11	15.7	2.0 (0.4)	2.0 (0.3)	59.3 (33.9)	52.7 (32.2)	29.1 (12.9)	28.8 (12.3)	191.3[§] (62.2)	154.1[§] (70.4)	38.9[§] (11.2)	30.1[§] (15.6)	17.1 (12.8)	16.2 (5.8)
*Micarea byssacea**	2	2.9	2.0 (0.5)	2.0 (0.3)	56.5 (23.3)	53.6 (32.6)	28.3 (21.2)	28.8 (12.2)	208.0 (149.9)	157.9[§] (67.4)	24.5 (2.1)	31.8[§] (15.5)	12.5 (2.6)	16.4 (7.3)
*Micarea contexta**	13	18.6	2.0 (0.3)	2.0 (0.3)	59.5 (22.8)	52.4 (34.1)	25.6 (12.1)	29.5 (12.3)	163.8[§] (70.6)	158.7[§] (70.7)	35.0[§] (6.8)	30.6[§] (16.8)	15.6 (6.2)	16.5 (7.5)
Micarea denigrata (LC)	2	2.9	2.0 (0.3)	2.0 (0.3)	47.5 (30.4)	53.9 (32.5)	20.4 (9.5)	29.1 (12.3)	168.0 (113.1)	159.5[§] (69.5)	28.5 (5.0)	31.6[§] (15.5)	15.7 (0.6)	16.3 (7.4)
Micarea elachista (LC)	19	27.1	1.8 (0.3)	2.0 (0.3)	61.5 (31.7)	50.8 (32.3)	40.3 (13.0)	24.5 (8.9)	194.4[§] (68.3)	151.6[§] (68.6)	39.2[§] (15.0)	29.4[§] (14.8)	16.6 (4.9)	16.2 (8.0)
Micarea eximia (VU)	5	7.1	1.9 (0.2)	2.0 (0.3)	52.2 (23.9)	53.8 (33.0)	24.8 (8.0)	29.1 (12.5)	154.2 (91.5)	160.5[§] (68.5)	30.2 (5.8)	31.7[§] (15.9)	19.3 (10.1)	16.1 (7.0)
Micarea globulosella (NT)	8	11.4	1.9 (0.3)	2.0 (0.3)	44.5 (25.0)	54.9 (33.1)	24.7 (8.4)	29.3 (12.6)	124.9 (33.4)	166.2[§] (73.2)	33.6 (16.5)	31.2[§] (15.2)	15.1 (6.5)	16.5 (7.4)
Micarea hedlundii (VU)	5	7.1	1.9 (0.2)	2.0 (0.3)	43.6 (35.7)	54.5 (32.2)	36.5 (11.9)	28.2 (12.2)	153.0[§] (17.0)	160.1[§] (71.3)	29.0[§] (8.5)	31.6[§] (15.5)	18.1 (3.6)	16.2 (7.5)
Micarea melaena (LC)	45	64.2	2.0 (0.3)	2.0 (0.3)	53.9 (30.9)	53.4 (35.3)	30.8 (13.1)	25.2 (9.8)	153.5[§] (64.2)	171.8[§] (80.4)	32.0[§] (13.8)	30.6[§] (18.2)	16.0 (5.4)	16.9 (9.9)
*Micarea melaeniza**	1	1.4	1.8 (0.0)	2.0 (0.3)	36.0 (0.0)	54.0 (32.4)	19.1 (0.0)	29.0 (12.3)	141.0 (0.0)	160.2[§] (70.6)	35.0 (0.0)	31.5[§] (15.4)	19.8 (0.0)	16.3 (7.3)
*Micarea micrococca**	4	5.7	2.0 (0.3)	2.0 (0.3)	46.0 (32.5)	54.2 (32.5)	21.9 (6.7)	29.2 (12.4)	162.5 (85.9)	159.6[§] (69.6)	48.0 (15.6)	30.2[§] (14.6)	14.1 (4.2)	16.4 (7.4)
Micarea micrococca agg., sp. nov.	1	1.4	1.6 (0.0)	2.0 (0.3)	19.0 (0.0)	54.2 (32.2)	19.1 (0.0)	29.0 (12.3)	83.0 (0.0)	161.4[§] (69.8)	31.0 (0.0)	31.5[§] (15.4)	12.4 (0.0)	16.4 (7.3)
Micarea misella (LC)	25	35.7	2.0 (0.3)	2.0 (0.3)	47.2 (32.1)	57.3 (32.2)	30.3 (13.8)	28.0 (11.4)	155.2[§] (83.5)	162.7[§] (61.4)	33.7[§] (12.6)	30.1[§] (16.9)	16.2 (6.5)	16.4 (7.7)
*Micarea nigella**	1	1.4	1.6 (0.0)	2.0 (0.3)	73.0 (0.0)	53.4 (32.4)	43.3 (0.0)	28.6 (12.2)	314.0 (0.0)	156.8[§] (67.2)	26.0 (0.0)	31.6[§] (15.4)	14.3 (0.0)	16.3 (7.3)
Micarea prasina (LC)	26	37.1	2.0 (0.3)	2.0 (0.3)	61.1 (33.3)	49.3 (31.2)	29.6 (14.2)	28.3 (11.1)	160.0[§] (74.8)	159.8[§] (68.7)	38.5[§] (13.9)	27.8[§] (14.8)	14.4 (5.1)	17.4 (8.1)
Micarea sp. nov. "nigrotomentosa"	1	1.4	1.8 (0.0)	2.0 (0.3)	30.0 (0.0)	54.1 (32.4)	51.6 (0.0)	28.5 (12.1)	NA	159.9[§] (70.0)	NA	31.5[§] (15.3)	23.0 (0.0)	16.2 (7.3)

(*continued on the next page*)

Species	n	%	DW diversity		Stumps (pc ha^{-1})		ø (cm)		AAD (y)		YFD (y)		Canopy (%)	
			1	0	1	0	1	0	1	0	1	0	1	0
Mollisia sp. 1	4	5.7	2.0 (0.5)	2.0 (0.3)	45.8 (29.2)	54.2 (32.6)	34.2 (15.9)	28.5 (12.1)	234.3[§] (119.3)	155.3[§] (65.1)	30.0[§] (15.1)	31.6[§] (15.4)	19.0 (7.8)	16.1 (7.3)
Mycena laevigata (LC)	1	1.4	2.5 (0.0)	2.0 (0.3)	22.0 (0.0)	54.2 (32.3)	29.9 (0.0)	28.8 (12.4)	302.9 (0.0)	157.1[§] (67.7)	27.0 (0.0)	31.6[§] (15.4)	16.5 (0.0)	16.3 (7.3)
Mycocalicium subtile "big"	19	27.1	2.0 (0.3)	2.0 (0.3)	47.0 (29.6)	56.2 (33.1)	22.9 (6.5)	31.0 (13.2)	138.5[§] (63.8)	169.3[§] (71.3)	29.7[§] (12.7)	32.4[§] (16.4)	18.0 (11.0)	15.7 (5.2)
Mycocalicium subtile "thin"	14	20.0	2.0 (0.4)	2.0 (0.3)	38.5 (30.9)	57.5 (31.7)	24.8 (8.8)	29.8 (12.9)	171.1[§] (76.7)	156.1[§] (68.3)	34.2[§] (16.5)	30.7[§] (15.0)	18.4 (5.3)	15.8 (7.6)
Mycocalicium subtile "smooth"	5	7.1	1.7 (0.1)	2.0 (0.3)	96.0 (21.9)	50.5 (30.7)	30.0 (8.9)	28.7 (12.5)	181.0 (51.7)	157.6[§] (71.7)	39.0 (8.9)	30.8[§] (15.6)	16.6 (9.1)	16.3 (7.2)
Mytilinidion mytilinellum (NE)	2	2.9	2.2 (0.2)	2.0 (0.3)	73.0 (46.7)	53.2 (32.1)	33.0 (14.1)	28.7 (12.3)	115.0[§] (0.0)	160.7[§] (70.4)	35.0[§] (0.0)	31.5[§] (15.4)	15.0 (2.1)	16.3 (7.4)
Mytilinidion rhenanum (NE)	1	1.4	1.8 (0.0)	2.0 (0.3)	30.0 (0.0)	54.1 (32.4)	27.4 (0.0)	28.8 (12.4)	136.0 (0.0)	160.3[§] (70.6)	9.0 (0.0)	31.9[§] (15.1)	12.7 (0.0)	16.4 (7.3)
Orbilia sp. 1	1	1.4	2.3 (0.0)	2.0 (0.3)	16.0 (0.0)	54.3 (32.2)	23.9 (0.0)	28.9 (12.3)	132.0 (0.0)	160.4[§] (70.6)	31.0 (0.0)	31.5[§] (15.4)	13.1 (0.0)	16.4 (7.3)
Orbilia sp. 2	2	2.9	2.2 (0.2)	2.0 (0.3)	72.0 (48.1)	53.2 (32.1)	28.4 (5.9)	28.8 (12.4)	118.0 (31.1)	161.5[§] (70.7)	35.0 (8.5)	31.4[§] (15.5)	8.6 (1.9)	16.5 (7.2)
Paxillus involutus (LC)	1	1.4	1.6 (0.0)	2.0 (0.3)	73.0 (0.0)	53.4 (32.4)	57.9 (0.0)	28.4 (11.8)	243.5 (0.0)	158.2[§] (69.7)	44.0 (0.0)	31.3[§] (15.3)	11.4 (0.0)	16.4 (7.3)
Peniophorella praetermissa coll. (LC)	4	5.7	1.7 (0.2)	2.0 (0.3)	51.3 (38.2)	53.9 (32.2)	25.6 (21.8)	29.0 (11.7)	149.5[§] (81.6)	160.5[§] (70.1)	29.7[§] (15.6)	31.6[§] (15.4)	14.9 (3.9)	16.4 (7.4)
Phialina sp. 1	1	1.4	2.3 (0.0)	2.0 (0.3)	16.0 (0.0)	54.3 (32.2)	30.4 (0.0)	28.8 (12.4)	145.0 (0.0)	160.1[§] (70.7)	46.0 (0.0)	31.3[§] (15.3)	14.7 (0.0)	16.3 (7.3)
Pholiota gummosa (LC)	1	1.4	2.5 (0.0)	2.0 (0.3)	22.0 (0.0)	54.2 (32.3)	40.4 (0.0)	28.6 (12.3)	312.0 (0.0)	156.9[§] (67.3)	14.0 (0.0)	31.9[§] (15.2)	29.6 (0.0)	16.1 (7.1)
Pholiota scamba (LC)	1	1.4	2.1 (0.0)	2.0 (0.3)	106.0 (0.0)	53.0 (31.9)	24.2 (0.0)	28.9 (12.3)	96.0 (0.0)	161.1[§] (70.1)	41.0 (0.0)	31.4[§] (15.4)	9.9 (0.0)	16.4 (7.3)
Piloderma bicolor (LC)	7	10.0	2.1 (0.4)	2.0 (0.3)	44.4 (32.3)	54.8 (32.4)	23.8 (7.5)	29.4 (12.6)	130.3 (69.2)	164.5[§] (69.7)	34.3 (19.7)	31.1[§] (14.7)	13.9 (4.3)	16.6 (7.5)
Porodaedalea pini (LC)	1	1.4	1.6 (0.0)	2.0 (0.3)	73.0 (0.0)	53.4 (32.4)	57.9 (0.0)	28.4 (11.8)	243.5 (0.0)	158.2[§] (69.7)	44.0 (0.0)	31.3[§] (15.3)	11.4 (0.0)	16.4 (7.3)
Postia sericeomollis (LC)	4	5.7	2.0 (0.2)	2.0 (0.3)	77.8 (36.3)	52.3 (31.7)	44.2 (6.3)	27.9 (11.9)	NA	159.9[§] (70.0)	NA	31.5[§] (15.3)	16.4 (5.2)	16.3 (7.4)

(*continued on the next page*)

Species	n	%	DW diversity		Stumps (pc ha^{-1})		ø (cm)		AAD (y)		YFD (y)		Canopy (%)	
			1	0	1	0	1	0	1	0	1	0	1	0
Pyrenomycete sp. 1	13	18.6	2.0 (0.3)	2.0 (0.3)	50.5 (32.4)	54.4 (32.5)	26.5 (7.9)	29.3 (13.1)	154.5§ (71.1)	161.3§ (70.5)	27.9§ (19.8)	32.4§ (14.1)	17.6 (8.2)	16.0 (7.1)
Pyrenomycete sp. 2	12	17.1	1.8 (0.3)	2.0 (0.3)	67.8 (42.9)	50.8 (29.3)	20.7 (7.7)	30.5 (12.4)	125.2§ (26.5)	169.2§ (75.2)	22.6§ (12.3)	33.8§ (15.2)	14.6 (4.2)	16.7 (7.7)
Pyrenomycete sp. 3	1	1.4	2.0 (0.0)	2.0 (0.3)	94.0 (0.0)	53.1 (32.1)	18.1 (0.0)	29.0 (12.3)	98.0 (0.0)	161.1§ (70.1)	6.0 (0.0)	32.0§ (15.0)	12.7 (0.0)	16.4 (7.3)
Pyrenomycete sp. 4	23	32.9	1.9 (0.3)	2.0 (0.3)	50.0 (31.5)	55.5 (32.8)	29.2 (13.0)	28.6 (12.0)	169.3§ (79.7)	154.0§ (63.8)	31.2§ (16.4)	31.7§ (14.8)	17.8 (7.2)	15.6 (7.3)
Pyrenomycete sp. 5	1	1.4	1.6 (0.0)	2.0 (0.3)	73.0 (0.0)	53.4 (32.4)	43.3 (0.0)	28.6 (12.2)	314.0 (0.0)	156.8§ (67.2)	26.0 (0.0)	31.6§ (15.4)	14.3 (0.0)	16.3 (7.3)
Resinicium bicolor (LC)	1	1.4	2.4 (0.0)	2.0 (0.3)	38.0 (0.0)	53.9 (32.5)	29.9 (0.0)	28.8 (12.4)	99.0 (0.0)	161.1§ (70.1)	32.0 (0.0)	31.5§ (15.4)	11.8 (0.0)	16.4 (7.3)
Resinicium furfuraceum (LC)	5	7.1	2.0 (0.1)	2.0 (0.3)	92.0 (19.2)	50.8 (31.3)	26.6 (6.5)	29.0 (12.6)	152.8§ (68.6)	160.4§ (70.8)	38.5§ (2.7)	31.0§ (15.7)	17.7 (8.8)	16.2 (7.2)
Sarea resinae (LC)	1	1.4	2.3 (0.0)	2.0 (0.3)	40.0 (0.0)	53.9 (32.5)	26.4 (0.0)	28.8 (12.4)	123.0 (0.0)	160.6§ (70.5)	8.0 (0.0)	32.0§ (15.1)	22.8 (0.0)	16.2 (7.3)
Tomentella sp. 1	2	2.9	2.3 (0.2)	2.0 (0.3)	53.5 (21.9)	53.7 (32.6)	28.5 (11.9)	28.8 (12.4)	130.4 (75.5)	161.0§ (70.3)	22.5 (23.3)	31.9§ (15.1)	14.6 (8.1)	16.4 (7.3)
Tomentella sp. 2	1	1.4	2.2 (0.0)	2.0 (0.3)	69.0 (0.0)	53.5 (32.5)	20.1 (0.0)	28.9 (12.3)	77.0 (0.0)	161.5§ (69.7)	39.0 (0.0)	31.4§ (15.4)	8.9 (0.0)	16.4 (7.3)
Trechispora farinacea (LC)	1	1.4	2.3 (0.0)	2.0 (0.3)	16.0 (0.0)	54.3 (32.2)	14.3 (0.0)	29.0 (12.2)	NA	159.9§ (70.0)	NA	31.5§ (15.3)	14.3 (0.0)	16.3 (7.3)
Trichaptum abietinum (LC)	1	1.4	2.2 (0.0)	2.0 (0.3)	69.0 (0.0)	53.5 (32.5)	24.5 (0.0)	28.9 (12.4)	81.0 (0.0)	161.4§ (69.8)	23.0 (0.0)	31.7§ (15.4)	10.1 (0.0)	16.4 (7.3)
Trichaptum fuscoviolaceum (LC)	11	15.7	1.9 (0.3)	2.0 (0.3)	58.2 (40.2)	52.9 (30.9)	26.6 (9.9)	29.2 (12.7)	138.7 (66.6)	165.5§ (70.6)	23.5 (11.4)	33.6§ (15.5)	14.1 (3.2)	16.7 (7.7)
Tubulicrinis subulatus (LC)	3	4.3	2.2 (0.4)	2.0 (0.3)	32.0 (8.7)	54.7 (32.6)	23.9 (1.8)	29.0 (12.5)	195.3 (71.0)	157.7§ (70.1)	49.7 (17.6)	30.5§ (14.6)	17.1 (4.5)	16.3 (7.4)
Xylodon asperus (LC)	2	2.9	2.3 (0.1)	2.0 (0.3)	27.0 (15.6)	54.5 (32.4)	23.4 (12.8)	29.0 (12.3)	140.0§ (0.0)	160.2§ (70.6)	29.0§ (0.0)	31.6§ (15.4)	10.8 (4.9)	16.5 (7.3)
Xylodon brevisetus (LC)	2	2.9	2.2 (0.0)	2.0 (0.3)	69.0 (0.0)	53.3 (32.6)	19.1 (7.7)	29.1 (12.3)	84.5 (5.0)	162.9§ (69.7)	24.0 (1.4)	31.8§ (15.5)	13.1 (4.3)	16.4 (7.3)
all trunks			2.0 (0.3)		53.7 (32.3)		28.8 (12.3)		159.9 (70.0)		31.5 (15.3)		16.3 (7.3)	

REFERENCES

Coppins, B.J., 1983. A taxonomic study of the lichen genus Micarea in Europe. Bull. Br. Museum (Natural Hist. Bot.) 11, 1–204.

Czarnota, P., 2007. The lichen genus Micarea (Iecanorales, Ascomycota) in Poland. Polish Bot. Stud. 23, 1–197.

Czarnota, P., Guzow-Krzemínska, B., 2010. A phylogenetic study of the Micarea prasina group shows that Micarea micrococca includes three distinct lineages. Lichenol. 42, 7–21. doi:10.1017/S0024282909990211

IUCN 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland.

Finnish Biodiversity Info Facility 2017. https://laji.fi/. Accessed 20.1.2017.

Knudsen, H., Vesterholt, J. (Eds.), 2008. Funga nordica. Nordsvamp, Copenhagen.

Rassi, P., Hyvärinen, E., Juslén, A., Mannerkoski, I., 2010. Suomen lajien uhanalaisuus – Punainen kirja 2010. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.

Royal Botanic Gardens Kew, Landcare Research-NZ, Institute of Microbiology, Chinese Academy of Science, 2016. Index Fungorum. http://www.indexfungorum.org/. Accessed 28.11.2016.

Tibell, L., 1999. Calicioid lichens and fungi. Nord. Lichen Flora 1, 20–94.

EFFECTS OF LOCAL FOREST CONTINUITY ON THE DIVERSITY OF FUNGI ON STANDING DEAD PINES

Saine Sonja, Aakala Tuomas, Purhonen Jenna, Launis Annina, Tuovila Hanna, Kosonen Timo & Halme Panu

Supplementary data 2. Responses of individual species

In the main text of this article we report the results of the community analyses. Here we report analyses on the responses of single species analyses using the same explanatory variables. We also briefly report the methods of the single species analyses and shortly discuss the results.

METHODS

Responses of single species were analyzed with a Mixed Effects Logistic Regression (n = 52). The aim was to study which environmental variables explain occurrences of each species the best. Species that occurred on ≥ 10 study trunks were included into the analysis (n = 14). A Mixed Effects Logistic Regression with a binomial distribution and a log-linear link function was conducted separately for each species. Explanatory variables were the same as in the GLMM (see the main text). Site and trunk identities were included into the model as hierarchically structured random effects by nesting trunks within sites. The model selection was conducted as in the GLMM. The analysis was performed in R (version 3.3.2; R Core Team, 2016) using function "glmer" from the package "lme4" (Bates et al., 2016).

RESULTS

Studied variables explained the presence of four species altogether. For the rest, the final models did not include any statistically significant variables. Occurrences of *Actidium hysterioides* were negatively affected by years from death (Table B.1). The final model also included dead wood diversity that had a marginally significant negative effect on the species (Table B.1). Occurrences of *Chaenothecopsis pusiola* were best explained by a negative effect of dead wood diversity, a negative effect of age at death, and a positive effect of years from death (Table B.1). These were all variables included in the final model. Canopy openness appeared to have a positive effect on the occurrences of *Glonium nitidum* (Table B.1). Number of stumps and years from death were the other variables included in the final model (Table B.1). The negative effect of

years from death was marginally significant (Table B.1). Occurrences of *Micarea elachista* were best explained by a negative effect of dead wood diversity (Table B.1). Another variable included in the final model was the number of stumps that had a marginally significant positive effect on the species as well (Table B.1).

Species final models of which included marginally significant effects of certain variables were *Micarea prasina* (a positive effect of years from death), *Mycocalicium subtile "thin"* (a negative effect of management intensity), Pyrenomycete sp. 4 (a negative effect of dead wood diversity, and a positive effect of canopy openness), and *Trichaptum fuscoviolaceum* (a negative effect of years from death) (Table B.1).

Table B.1. Results from the Mixed Effects Logistic Regression for individual species (n = 52 for each). Cells show estimates (B), standard errors (SE), z values, and statistical significances (P). Dead wood (DW) diversity was calculated with Shannon's diversity index. The units used for variables are in brackets. Abbreviations: YFD = years from death, AAD = age at death, stumps = management intensity, canopy = canopy openness.

Species		B	SE	z value	P
Actidium hysterioides	(Intercept)	-1.72	0.76	-2.27	0.023
	DW diversity	-1.09	0.62	-1.75	0.081
	YFD (y)	-1.42	0.69	-2.07	0.039
Chaenothecopsis pusiola	(Intercept)	-0.75	0.35	-2.16	0.031
	DW diversity	-0.76	0.37	-2.05	0.041
	AAD (y)	-0.81	0.41	-1.97	0.049
	YFD (y)	0.97	0.41	2.38	0.017
Glonium nitidum	(Intercept)	0.18	0.61	0.30	0.763
	Stumps (pc ha^{-1})	1.00	0.67	1.48	0.138
	YFD (y)	-1.04	0.55	-1.90	0.058
	Canopy (%)	1.75	0.78	2.25	0.025
Micarea contexta	(Intercept)	-1.73	0.69	-2.51	0.012
	YFD (y)	0.55	0.44	1.25	0.213
Micarea elachista	(Intercept)	-3.19	0.92	-3.46	< 0.001
	DW diversity	-2.58	0.92	-2.81	0.005
	Stumps (pc ha^{-1})	0.84	0.47	1.80	0.072
Micarea melaena	(Intercept)	0.81	0.46	1.77	0.076
	AAD (y)	-0.43	0.43	-1.01	0.315
Micarea misella	(Intercept)	-0.59	0.41	-1.44	0.149
	YFD (y)	0.12	0.34	0.35	0.728
Micarea prasina	(Interept)	-1.20	0.71	-1.69	0.091
	YFD (y)	0.74	0.44	1.68	0.093
Mycocalicium subtile "big"	(Intercept)	-0.86	0.32	-2.74	0.006
	AAD (y)	-0.51	0.36	-1.44	0.150
Mycocalicium subtile "thin"	(Intercept)	-2.34	1.15	-2.03	0.043
	Stumps (pc ha^{-1})	-1.70	0.99	-1.72	0.085
Pyrenomycete sp. 1	(Intercept)	-1.31	0.34	-3.82	< 0.001
	Canopy (%)	0.33	0.39	0.85	0.398
Pyrenomycete sp. 2	(Intercept)	-2.46	2.55	-0.96	0.335
	DW diversity	-1.15	1.28	-0.90	0.370
	AAD (y)	-1.25	1.33	-0.94	0.346
	YFD (y)	-1.04	1.21	-0.86	0.388
Pyrenomycete sp. 4	(Intercept)	-0.65	0.44	-1.49	0.136
	DW diversity	-0.82	0.43	-1.94	0.053
	Canopy (%)	0.99	0.51	1.93	0.053
Trichaptum fuscoviolaceum	(Intercept)	-1.71	0.61	-2.83	0.005
	YFD (y)	-0.84	0.49	-1.70	0.089

DISCUSSION

Occurrences of *Chaenothecopsis pusiola* showed a positive association with time since tree death, and for *Micarea prasina* the positive effect was nearly statistically significant. The species occurred more likely on trunks that had died longer time ago. The positive effect of time since tree death on *C. pusiola* might be explained by its suggested parasitic relationship with lichens and non-symbiotic algal colonies (Tuovila, 2013). Also, more suitable habitats form with time, as the species prefers decorticated wood (Lõhmus and Lõhmus, 2001). *M. prasina* is a crustose lichen especially common in old-growth forests (Stenroos et al., 2015). Presumably, this slow-growing species (Stenroos et al., 2011) benefits from long periods since tree death like lichens in general.

Years from death had a negative effect on pyrenomycetes *Actidium hysterioides* and *Glonium nitidum* and polypore *Trichaptum fuscoviolaceum,* yet the effect was not statistically significant for the latter two. All these species might be early successional species. Many pyrenomycetes latent in the wood are abundant in initial decay stages (Heilmann-Clausen, 2001; Hendry et al., 2002). Additionally, increasing moisture content with proceeding decomposition (Sollins et al., 1987) might hinder these species adapted to dry conditions (Boddy et al., 1989, 1985). *T. fuscoviolaceum* is a pioneer species that is often among the initial decomposers (Niemelä et al., 1995; Renvall, 1995). The species loses in competitive ability or due to depleting resources when late-stage specialists colonize the community (Rayner and Boddy, 1988; Stokland et al., 2012).

C. pusiola responded negatively to the increasing trunk age at death. The species seems to occur frequently on decorticated, decayed surfaces on the base of the boles (Hanna Tuovila, personal communication). Such microhabitat patches might be more common in younger trunks due to the differences in decay succession. Old standing kelo trees, for example, rarely offer such microhabitats. Therefore, the species might prefer trunks that have died at younger age.

Dead wood diversity had a negative effect on *C. pusiola, Micarea elachista*, *A. hysterioides* and Pyrenomycete sp. 4, although the effect was not statistically significant for the latter two. *C. pusiola* also occurs in managed forests as long as suitable substrates are available (Hanna Tuovila, personal communication), and therefore the species might not be dependent on old-growth forests *per se*. The

negative effect on *M. elachista* might indicate that the species is not dead wood dependent as such since it can also grow on old living trees (Coppins, 1983; Czarnota, 2007). Like many pyrenomycetes, also *A. hysterioides* and Pyrenomycete sp. 4 might be associated with early stages of decomposition (Heilmann-Clausen, 2001; Hendry et al., 2002). The emergence of more specialized species with increasing dead wood diversity might have an adverse effect on these species.

Pyrenomycetes *G. nitidum Ellis* and Pyrenomycete sp. 4 showed a positive response to canopy openness, yet the effect was not statistically significant for the latter. Pyrenomycetes in general are characterized by high resistance to water stress (Boddy et al., 1989, 1985). Consequently, the competitive superiority of these species in dry circumstances might explain the result.

Altogether, negative responses to local continuity were predominant among individual species. Such responses could be expected from generalists that lose to late-stage specialists in competitiveness (Marvier et al., 2004). Kruys et al. (1999) hypothesized that species dependent on dead wood continuity require habitats that are scarce within a landscape. Presumably, these species are specialists and rare. In our study, such species did not probably have enough occurrences to be included in the analyses. Some of these species might be *e.g.* veteran tree specialists that inhabit the oldest trunks for which the age parameters were not successfully quantified. Therefore, more research on rare and specialized species is required to clarify their relationship with local continuity.

REFERENCES

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Grothendieck, G., Green, P., 2016. lme4: Linear Mixed-Effects Model using 'Eigen' and S4, version 1.1-12. https://cran.r-project.org/web/packages/lme4/lme4.pdf. Accessed 30.11. 2016.

Boddy, L., Gibbon, O.M., Grundy, M.A., 1985. Ecology of Daldinia concentrica: effect of abiotic variables on mycelial extension and interspecific interactions. Trans. Br. Mycol. Soc. 85, 201–211. doi:10.1016/S0007-1536(85)80183-2

Boddy, L., Owens, E.M., Chapela, I.H., 1989. Small scale variation in decay rate within logs one year after felling: effect of fungal community structure and moisture content. FEMS Microbiol. Ecol. 62, 173–184. doi:10.1016/0378-1097(89)90110-9

Coppins, B.J., 1983. A taxonomic study of the lichen genus Micarea in Europe. Bull. Br. Museum (Natural Hist. Bot. 11, 1–204.

Czarnota, P., 2007. The lichen genus Micarea (Iecanorales, Ascomycota) in Poland. Polish Bot. Stud. 23, 1–197.

Heilmann-Clausen, J., 2001. A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycol. Res. 105, 575–596. doi:10.1017/S0953756201003665

Hendry, S.J., Boddy, L., Lonsdale, D., 2002. Abiotic variables effect differential expression of latent infections in beech (Fagus sylvatica). New Phytol. 155, 449–460.

Kruys, N., Fries, C., Jonsson, B.G., Lämås, T., Ståhl, G., 1999. Wood-inhabiting cryptogams on dead Norway spruce (Picea abies) trees in managed Swedish boreal forests. Can. J. For. Res. 29, 178–186. doi:10.1139/x98-191

Lõhmus, P., Lõhmus, A., 2001. Snags, and their lichen flora in old Estonian peatland forests. Ann. Bot. Fenn. 38, 265–280.

Marvier, M., Kareiva, P., Neubert, M.G., 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Anal. 24, 869–878. doi:10.1111/j.0272-4332.2004.00485.x

Niemelä, T., Wallenius, T., Kotiranta, H., 1995. Interactions of fungi at late stages of wood decomposition. Ann. Bot. Fenn. 32, 141–152.

Rayner, A.D.M., Boddy, L., 1988. Fungal decomposition of wood: its biology and ecology. John Wiley & Sons, Chichester.

R Core Team. 2016. R: A language and environment for statistical computing. Version 3.3.2. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/. Accessed 30.11. 2016.

Renvall, P., 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35, 1–51.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., Spycher, G., 1987. Patterns of log decay in old-growth Douglas-fir forests. Can. J. For. Res. 17, 1585–1595. doi:10.1139/x87-243

Stenroos, S., Ahti, T., Lohtander, K., Myllys, L., Haikonen, V. (Eds.), 2011. Suomen jäkäläopas. Kasvimuseo, Luonnontieteellinen keskusmuseo LUOMUS, Helsinki.

Stenroos, S., Velmala, S., Pyhälä, J., Ahti, T. (Eds.), 2015. Suomen rupijäkälät. Luonnontieteellinen keskusmuseo LUOMUS, Helsinki.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, UK.

Tuovila, H., 2013. Sticky business – diversity and evolution of Mycocaliciales (Ascomycota) on plant exudate. University of Helsinki.

IV

VARYING EFFECTS OF FOREST NATURALNESS ON DIFFERENT MORPHO-GROUPS OF WOOD-INHABITING FUNGI

by

Purhonen Jenna, Abrego Nerea, Komonen Atte, Huhtinen Seppo, Kotiranta Heikki, Læssøe Thomas & Halme Panu 2018

Manuscript

Request a copy from author.

V

MORPHOLOGICAL TRAITS PREDICT HOST-TREE SPECIALIZATION IN WOOD-INHABITING FUNGAL COMMUNITIES

by

Purhonen Jenna, Ovaskainen Otso, Halme Panu, Komonen Atte, Huhtinen Seppo, Kotiranta Heikki, Læssøe Thomas & Abrego Nerea 2018

Manuscript

Request a copy from author.