Dissertationes Forestales 39

Conservation of polypore diversity in managed forests of boreal Fennoscandia

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Academic dissertation

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Title: Conservation of polypore diversity in managed forests of boreal Fennoscandia

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ABSTRACT

In this thesis patterns of polypore assemblages are described along the gradients of forest succession and naturalness, and the effectiveness of some biodiversity-oriented forestry methods for maintaining the diversity of polypores in managed forests is evaluated. The thesis is based on four different data sets collected in eastern Finland 1996-2005. The data include a total of 19 617 records of fungi (based on presence of fruiting bodies) representing 129 species of polypores and 133 species of corticiaceous fungi.

The main findings of the thesis are as follows:

1) For wood-inhabiting fungi, in managed as well as in natural forests, the most species-rich phase of forest succession is the first stage after a major disturbance (wildfire or clear-cutting). The fungal assemblages at the first stage of forest succession are distinctive, particularly in natural forests, compared to the assemblages at later successional stages.

2) After the first stage of succession, the level of forest naturalness is more important than the successional stage in determining the diversity of polypores. Particularly threatened species suffer with increasing levels of management intensity, and in the most intensively managed forests, no threatened species can be found.

3) Fallen retention aspens can be suitable habitats for several polypore species, including many red-listed species.

4) Woodland key habitats, as defined in the Finnish Forest Act, can support several polypore species, but provide little help for red-listed species.

5) The short-term effects on polypores from logging are more dramatic than the effects of fire. On the time scale of four years, logging changes the species composition of polypore assemblages, increases dominance and increases the overall polypore abundance, but decreases the proportion of red-listed and species designated as biodiversity indicators.

The results presented in this thesis underline the fundamental importance of dead wood, its amount and diversity, in maintenance of species diversity in managed forests. Of the current biodiversity-oriented forestry practices, tree retention (at clear-cut sites) can be an effective way of supporting polypore diversity, including red-listed species. However, current retention levels need to be increased to support diversity. The short-term value of “woodland key habitats” and prescribed burning seem to be limited with regards to polypores. The long-term effects, however, may prove to be different. Measures enhancing the diversity of polypores are also likely to improve the living conditions of other taxa dependent on dead trees or large living trees, thus supporting the maintenance of the most threatened part of species diversity in the Fennoscandian boreal forests.

Keywords: Biodiversity, Dead wood, Fire, Forest succession, Fungi, Tree retention, Woodland key habitat

ACKNOWLEDGEMENTS

I can recall swearing countless times in my ‘previous life’ that I would never start working on a PhD thesis, because I had so many more important things to do in my life. Yet, now that it’s time to say goodbye to my status as a PhD student, I find it hard to imagine another job that I’d enjoy as much as being a researcher.

My deepest gratitude goes to Jari Kouki who offered me the opportunity to change my attitude towards PhD studies. Jari has been an excellent supervisor; encouraging and supporting, always finding time to fix my unsolved problems, providing quick comments on manuscripts, and easily engaging in philosophical discussions. My other supervisor, Pertti Renvall, also deserves my warmest thanks. Pertti has been patient with my loads of to-be-identified specimens. He introduced me to the art of microscopy and guided me into the field of mycology, along with correcting the inaccurate mycological terminology of my manuscripts.

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LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following papers referred to in the text by the Roman numerals I-IV:

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

II Junninen, K., Penttilä, R. and Martikainen, P. 2007: Fallen retention aspen trees on clear-cuts can be important habitats for red-listed polypores: a case study in Finland. Biodiversity and Conservation 16:475-490.

III Junninen, K. and Kouki, J. 2006: Are woodland key habitats in Finland hotspots for polypores (Basidiomycota)? Scandinavian Journal of Forest Research 21:32-40.

IV Junninen, K., Kouki, J. and Renvall, P. Restoration of natural legacies of fire and conservation of wood-decaying fungi in European boreal forests: large-scale experimental approach. Submitted manuscript.

Articles I-III are reproduced with the kind permission of the publishers: Blackwell Publishing (I), Springer (II), and Taylor & Francis (III).

Contributions of the authors to the articles and to the manuscript.

	I	II	III	IV
Original idea	JK	PM	KJ	JK
Study design	JK, KJ	PM, RP	KJ, JK	JK, KJ
Data collection	MS, KJ, JK	RP, PM	KJ	KJ
Species identification	HK, KJ, PR	RP	KJ, PR	KJ, PR
Data analysis	KJ, JK	KJ, PM	KJ, JK	KJ
Manuscript preparation	KJ, JK	KJ, PM, RP	KJ, JK	KJ, JK, PR

HK, Heikki Kotiranta; JK, Jari Kouki; KJ, Kaisa Junninen; MS, Maarit Similä; PM, Petri Martikainen; PR, Pertti Renvall; RP, Reijo Penttilä. Other contributors are acknowledged in the relevant articles and in the manuscript.

TABLE OF CONTENTS

ARTICLES I-IV

1 INTRODUCTION

1.1 Biodiversity

“Biodiversity” is a fascinating concept embracing “all life on the Earth”. Even before the introduction of the word “biodiversity” (Wilson 1988), the concept existed in the form of “biological diversity”, “ecological diversity” (Magurran 1988) or “species diversity” (Pianka 1966) and attracted many biologists. The Convention on Biological Diversity (negotiated at United Nations Conference on Environment and Development 1992 in Rio de Janeiro) raised the concept into common knowledge and inspired an overwhelming number of studies addressing its different aspects (Haila & Kouki 1994). The main aim of these studies has been to document the diversity of life (other than human) on the Earth and find ways to maintain it. My thesis contributes to this never-ending task of biologists, giving a fraction of understanding of what are the patterns of polypore diversity in boreal forests and what can be done in order to maintain this diversity in our managed forest landscapes.

The concept of biodiversity can be defined more explicitly by recognizing three hierarchical elements in it. These are often referred to as genetic diversity, organismal (or species) diversity and ecological (or ecosystem and habitat) diversity (Heywood & Watson 1995). Although all these levels can be considered equally important, one measure of biodiversity has arisen above the others: the species diversity. Species diversity is most often described simply as the number of species, or species richness (e.g. Gaston 1996; Tokeshi 1999). Although species richness covers only a part of the broader concept of species diversity, there are several good reasons why it deserves to be so widely applied (Gaston & Spicer 2004): species richness is a relatively unambiguous measure and relatively easy to measure; a lot of information on species already exists and this information is applied in practice, e.g. in management of natural resources or in legislation. Also, global patterns of species diversity are rather well known for some taxa, particularly for terrestrial vertebrates.

Besides climate change, the loss of biodiversity is clearly the most urgent and alarming human-induced global trend. After the Convention on Biological Diversity, international concern has been further manifested by the Biodiversity Target 2010 (agreed on at the World Summit on Sustainable Development in Johannesburg 2002) and by EU action plan to halt biodiversity loss by 2010 (“Message from Malahide” 2004). Yet, in international assessments it has been estimated that today we are losing species at the rate that is up to 1000 times higher than the rate that has been detected in fossil records during the geological history (Heywood & Watson 1995; Millenium Ecosystems Assessment 2005). This rate of extinctions is expected to further increase, and the current period has been described as the sixth major extinction era on the Earth. The most important reason for loss of species is loss of their habitats due to human exploitation (Heywood & Watson 1995).

Conservation of biodiversity or species richness is not a simple task, even from purely ecological perspective. Global hotspots of species richness do not necessarily capture the hotspots of rare or endemic species (Prendergast et al. 1993; Orme et al. 2005), and despite recent conservation efforts, some critical threshold levels for existence of many species may have already been passed (Brooks et al. 1999; Cowlishaw 1999; Helm et al. 2006; Vellend et al. 2006). Furthermore, we do not know the functional importance of the lost species, or the way ecosystems will respond to reductions in diversity (McCann 2000;

Loreau et al. 2001; McCann 2007). And there is no restoration method that would bring extinct species back.

On a global scale, the greatest species richness is known to exist in the tropics, with the number of species decreasing towards higher latitudes (e.g. Rohde 1992). Some groups of species, however, show an opposite biogeographical pattern (Kouki 1999), thus emphasizing the importance of complementary approach in species conservation also on the global scale. Boreal forests, for example, although not as species-rich as tropical forests, contain some special features and conditions not met elsewhere. One feature of special importance for boreal species diversity is dead wood that decomposes at a relatively slow rate due to cold climate and, thus, provides a diversity of habitats for a diversity of species (Hanski & Hammond 1995; Renvall 1995). This diversity includes wood-decomposing fungi, the main actors of my thesis.

1.2 Polypore fungi – the study organisms

Polypores (poroid Basidiomycota) are a polyphyletic group of basidiomycetous fungi the spores of which develop in pores; excluding boleti, and including some lamellate species with hard fruiting bodies. Although phylogenetically diverse, functionally polypores are a more or less homogeneous group, with a great majority being decomposers of woody material (e.g. Rayner & Boddy 1988). A functionally closely related group of species is the corticiaceous fungi that are separated from polypores by different appearance of fruiting bodies (non-poroid hymenial surface). The total number of polypore species on the Earth has been estimated to be around 1500 (Leif Ryvarden, pers. comm.), and for Finland a recent revision of the check-list revealed a total of 230 species (Niemelä 2005).

In boreal coniferous forests, polypores are the most important decomposers of dead trees (Renvall 1995). Many of the conifer-decaying polypores are brown-rot fungi, particularly in dry pine forests. Brown-rot fungi decompose only carbohydrate components of wood, leaving most of the lignin unaltered, and produce residues that may remain stable in forest soils; contrary to white-rot fungi that decompose all major components of wood equally and eventually decay the wood completely. Brown-rot logs are known to provide favorable microsites for the establishment of conifer seedlings in boreal forests (McCullough 1948; Harmon & Franklin 1989; Hofgaard 1993). This may be related to the quality of the decay: brown-rot residues improve soil conditions including water holding capacity, pH and soil temperature (e.g. Ryvarden & Gilbertson 1993 and references therein). Furthermore, decayed wood provides important substrate for ectomycorrhizal development (e.g. Harvey et al. 1979). Thus, it is not only that trees facilitate the existence of polypores, but to some extent also the trees depend on polypores, particularly in northern regions.

1.3 Dead wood in forests – the study habitat

Decomposition of a tree is a process that inevitably leads to disappearance of the decomposer’s habitat. To persist, the decomposer species must be able to disperse to a new habitat patch (dead wood unit of suitable quality) within a finite time-scale. In forests under natural disturbance dynamics without human exploitation of wood, the input of dead wood is – although stochastic locally – more or less constant in relation to the life-spans and dispersal abilities of decomposer species (Kuuluvainen 1994; Renvall 1995; Jonsson 2000; Stokland 2001; Rouvinen & Kouki 2002). This relative predictability and abundance of dead-wood habitats has provided good possibilities for evolution of diverse decomposer communities through resource partitioning and niche specialization (*sensu* MacArthur & MacArthur 1961).

Intensive commercial forest management has caused a dramatic decline in the amount of dead wood in forests during the last few decades, particularly in Fennoscandian countries (Kalliola 1966; Esseen et al. 1992; Linder & Östlund 1998; Fridman & Walheim 2000; Siitonen 2001). This, in turn, has resulted in decline in decomposers and other species dependent on dead wood, the "saproxylic" species (*sensu* Speight 1989). Today many of them are included in national red lists of threatened species (Bendiksen et al. 1998; Gärdenfors 2000; Rassi et al. 2001); in Finland, for example, 35% of the polypores known for the country are red-listed (Rassi et al. 2001). Improving the situation of these species is one of the biggest challenges for the Fennoscandian countries in trying to fulfill the objectives of international initiatives of biodiversity conservation (Hawksworth 1997).

The patchy and ephemeral nature of dead wood imposes particular challenges to conservation of species dependent on it (Siitonen 2001; Jonsson et al. 2005). Furthermore, "dead wood" is not a homogeneous habitat type but rather a collective term – similar to "forests" – for a range of habitats. These habitat types, or microhabitats, include, for example, different tree species of different trunk diameters at different stages of decay (e.g. Harmon et al. 1986; Renvall 1995). During the decomposition process, the decomposers further alter the structure, moisture and chemistry of the decaying trees and thus create new niches for other saproxylic species. Also, the variety of decomposition pathways involves successions of different fungal species, and this also contributes to the variety of microhabitats in the trunks at advanced stages of decay (Renvall 1995). Maintaining all saproxylic species requires maintaining the full ranges of different types of dead wood habitats, in sufficient quantities and without breaks in continuity.

Maintaining continuity of some dead wood types may be challenging even in national parks and other large forest reserves (Kouki et al. 2004), but it can be even more difficult in forests managed for wood-production. Yet, because of the uneven distribution of reserves and the relatively small area covered by them, the role of the matrix (i.e. the managed forest landscape surrounding the reserves) in maintaining the biodiversity of Fennoscandian forests is important and involves consideration of spatial scales of the focal species' habitats. (Mönkkönen & Reunanen 1999; Kouki et al. 2001). For example, for many saproxylic species, this scale is the occurrence of individual dead trees of suitable quality within the species' dispersal distance, instead of the occurrence of old-growth forest patches, which might be the relevant scale for some other species.

So far, the efforts in increasing dead wood in managed forests have concentrated in increasing the overall amount of dead wood without paying much attention to its different types (except from the economic point of view). The efforts include tree retention and creation of high stumps in clear-cut areas (Halpern & McKenzie 2001; Vanha-Majamaa & Jalonen 2001; Lindhe et al. 2004), introduction of controlled burning as a restoration method in reserves (Kuuluvainen et al. 2002; Hyvärinen et al. 2006), and protection of small-scale forest patches via ecological landscape planning and legislation (Nitare & Norén 1992; Aasaaren & Sverdrup-Thygeson 1994; Meriluoto & Soininen 1998). At the same time, however, there is an increasing demand for biofuels, including harvesting of logging residues and even cut stumps for energy use – a practice that at least partly counteracts the efforts of increasing the amount of dead wood in Fennoscandian managed forests (Rudolphi & Gustafsson 2005).

1.4 Aim of the thesis

Despite the recent efforts to maintain diversity of polypores and other saproxylic species also in forests managed for wood production, intensive management still poses serious challenges for survival of viable polypore populations in Fennoscandian forests (Spence 2001). Obviously, there are still several research questions that need to be rigorously addressed to develop and implement ecologically sound management and conservation principles. To meet these challenges, this thesis provides basic information on community ecology of polypores and connects this information with practical forest management methods currently applied in Finnish forests.

This thesis explores the structure of polypore assemblages at different successional stages of forest and at different levels of forest naturalness, and evaluates some new, more biodiversity-oriented forestry methods in their effectiveness towards protecting the diversity of polypores. The thesis also aims at addressing the practical implications for biodiversity conservation in managed forests.

More specifically, the questions addressed in the thesis are

1) How do, if at all, assemblages of wood-decaying fungi change along the gradients of forest succession and naturalness? How can these results be applied towards biodiversity conservation?
2) What is the importance of retention of aspen trees in protecting the diversity of polypores?
3) What is the importance of woodland key habitats, as defined in the Finnish Forest Act, in protecting the diversity of polypores?
4) What is the importance of fire in promoting the diversity of polypores?

2 MATERIAL AND METHODS

This thesis is based on four different data sets (Table 1) collected in eastern Finland, southern boreal zone (II, III) or in transition between southern and middle boreal zones (I, IV) (*sensu* Ahti et al. 1968) (Fig.1). The landscape of the study area is dominated by managed forests fragmented by lakes, open mires, cultivated land and sparse settlements. The main tree species are Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.) and birches (*Betula pendula* Roth. and *B. pubescens* Ehrh.). The history of commercial forest utilization in eastern Finland is relatively short, because of the location of the areas beyond the limit of economically profitable logging until the late 20th century (Lihtonen 1949; Kalliola 1966). Because of this, particularly in areas close to the eastern (Russian) border, several old-growth patches and reserves are located within the managed forest landscape. Thus, the continuity of structural characteristics of natural forests and the continuity of species dependent on those structures are still relatively well preserved in the study region compared to other parts of southern boreal zone in Finland. This makes it possible to study not only the common forest-dwelling species but also the red-listed and other species dependent on characteristics typical of natural forests.

The data include a total of 19 617 records of 262 species of fungi (of which 129 species of polypores) (Appendix). The data are records of fungal fruiting bodies (sporocarps) of polypores on wood (in paper I, corticiaceous fungi were also included). The fruiting bodies were recorded on sampling plots of fixed area (I, III, IV) or on a fixed number of trunks (II)

(Table 1). For large-scale ecological field studies documenting the presence of fruiting bodies is in practice the only method that has been and can be used, although it omits the species and individuals not fruiting at the time of the inventory. To alleviate this problem, all data were collected during the best fruiting season of polypores in late August–October. Also, comparisons between data sets collected in different years were avoided or analyzed with care, because variation in weather conditions may cause variation in fruiting body production. Yearly fruiting body production of wood-living polypores, however, has been found to be relatively stable compared to that of soil-inhabiting or corticiaceous fungi (Hintikka 1993; Berglund et al. 2005) and, thus, the yearly variation within the present data sets (I, II, IV) should not have been a major problem.

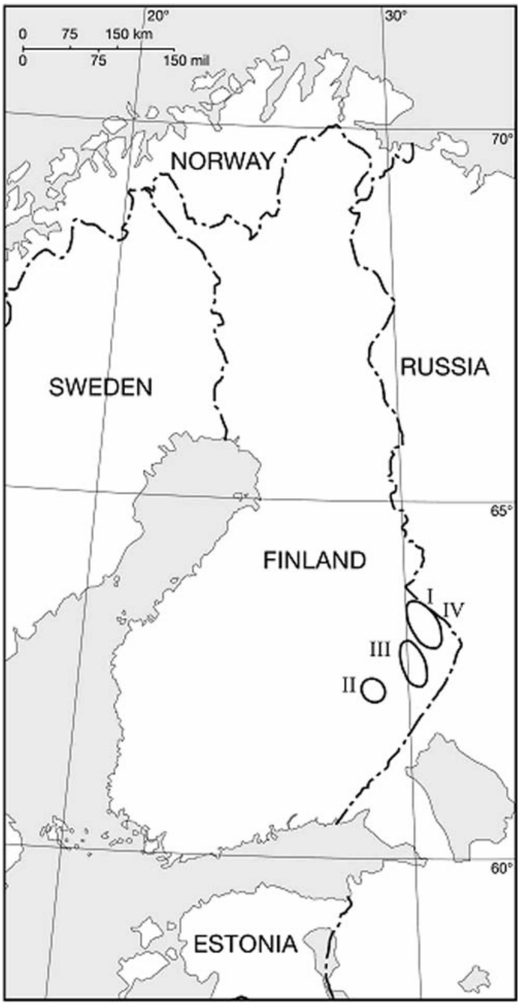

Figure 1. Location of the study areas. Roman numerals I-IV refer to the original research articles included in the thesis. Although I and IV are denoted with the same location, the data for the two articles originate from different forest stands.

Table 1. Sampling years, sampling efforts and polypore data used for papers I-IV.

	I	II	III	IV
Sampling years	1999, 2002	1996, 1997	2003	2000, 2002, 2005
Total area sampled (ha)	12.9	-	13.8	24.0 [a]
Area of one sampling plot (ha)	0.314	-	0.04 - 0.2	1.0
Number of trunks sampled	-	110	-	-
Number of records	5328 [b]	499	2345	11445
Number of species	195 [c]	46	98	104

[a] the same sites were sampled three times (different years)

[b] 1391 records of polypores and 3937 records of corticiaceous fungi

[c] 62 species of polypores and 133 species of corticiaceous fungi

In paper I, assemblages of polypores and corticiaceous fungi along the gradients of forest naturalness and succession were studied by establishing replicated series of study plots at three levels of forest naturalness – or management intensity – and at five stages of forest succession in pine-dominated forests. Polypores were found to reflect the effects of forest management more clearly than the corticiaceous fungi, and, on the other hand, corticiaceous fungi were found to be very laborious to collect and identify. Thus, polypores were identifed as more ‘cost-efficient’ for the further large-scale field studies. Based on this study, the general patterns of polypore species diversity and of composition of polypore assemblages could be detected. This background information is essential when assessing the effects of new forest management methods that aim at decreasing the impacts of forestry on biodiversity.

In papers II, III and IV, the importance of new forest management measures were studied in relation to polypore diversity. The measures studied include retention trees at clear-cuts (II), protection of woodland key habitats as defined in the Finnish Forest Act (III), and use of controlled burning of logging areas as a silvicultural method and, of unlogged forests as a restoration method (IV).

In all studies included in this thesis, three main aspects were analyzed to describe the patterns of polypore assemblages, or polypore diversity: (1) the total number of species and records of polypores, (2) the number of species and records of threatened or red-listed species (as defined in Rassi et al. 2001) and (3) the composition (similarity) of species assemblages. The differences between groups were detected by using ANOVA and non-parametric statistical tests, and relative similarities within and between groups were examined with detrended correspondence analysis (DCA ordination) and with diversity indices.

3 MAIN RESULTS AND DISCUSSION

3.1 Early successional forests are species-rich and distinctive in polypore species composition

An unexpected pattern of polypore species-richness was found in the study presented in paper I: The earliest stage of forest succession following a major disturbance was the most species-rich of all successional stages. This pattern was found in the most natural-like forests regenerating after a wildfire, as well as in intensively managed forests after clear-cutting, and the pattern was even more clear when corticiaceous fungi were also taken into account. A likely explanation for the finding lies in the evolutionary history of polypores as wood-decaying fungi: polypore species richness would be expected to be highest when the amount (and diversity) of dead wood is highest and, in natural forests, this is the period of early succession following a major disturbance like a wildfire or a windstorm (Lee et al. 1997; Uotila et al. 2001; Pedlar et al. 2002). Furthermore, the composition of polypore assemblages of early successional forests was found to be very different from those at later stages of succession, particularly in natural forests (I, IV). This clearly reflects the unique conditions in forests at early stage of succession: abundance of fresh dead wood available in extreme microclimatic conditions – a situation never present at later stages of succession. Of these two factors, the resources (abundance of fresh dead wood) is probably of much greater importance than the environment (microclimatic conditions) since the fruiting body production of most polypore species seems to be more or less indifferent to the general microclimatic conditions of the habitat (Martikainen et al. 2000; Lindhe et al. 2004; Penttilä 2004; Heilmann-Clausen et al. 2005, I, II).

3.2 Level of naturalness determines polypore diversity in forests at later stages of succession

In the forest succession following the first, open stage, forest naturalness was found to be more important than the successional stage in determining the diversity of polypores (I). Particularly threatened species suffered with increasing level of management intensity, and in most intensively managed forests, no threatened species were found. This trend is obviously related to dead wood, its amount, quality and/or continuity (Bader et al. 1995; Renvall 1995; Ohlson et al. 1997; Lindblad 1998; Sippola & Renvall 1999; Humphrey et al. 2000; Nordén & Paltto 2001; Sippola et al. 2001; Groven et al. 2002; Heilmann-Clausen & Christensen 2004; Penttilä et al. 2004). For the amount of dead wood, it has been estimated that 20 m^3 of dead wood per hectare may represent an approximate threshold value below which the persistence of threatened polypores becomes unlikely (Penttilä et al. 2004). In intensively managed forests, the amount of dead wood is largest after the pre-commercial thinning of young forest, provided that the cut trees are left on the forest floor, but even then the total amount stays below 5 $m^3 ha^{-1}$ (I), i.e. clearly below the suggested threshold value for threatened polypores. The diversity of dead wood qualities (e.g. tree species, diameter, decay stage) usually correlates to the amount of dead wood (Penttilä et al. 2004) and thus further supports the diversity of polypores.

3.3 Fallen retention aspens can host red-listed polypores

Retention trees left at clear-cut areas are supposed to alleviate the negative effects of logging on biodiversity by ‘lifeboating’ species over the regeneration phase of the forest and by enriching the structure of the reestablished forest stand (Franklin et al. 1997). Most polypore species can utilize retention trees (for sexual reproduction) only after the trees have fallen and started to decay; but to what extent this actually happens has remained largely unstudied (but see Siitonen et al. 2006). According to paper II, large fallen retention aspens can be important habitats for several polypore species, including many red-listed species, at least when the volume of retention trees is around 60 m^3 ha^{-1} and there are good dispersal sources of polypores near the logging areas.

Thus, retention of large trees in sufficient numbers seems to be an ecologically effective way of supporting several polypore species in managed forests. Apparently retention trees not only ‘lifeboat’ the species over the period of little or no dead wood available but actually provide habitat for species that have evolved to utilize the conditions of the first stage of succession in natural forest ecosystems. Without logging (or other disturbance such as fire or windstorm) no habitat would be available for species that produce fruiting bodies in open, sunny conditions rather than within shaded forests. It is important to note, however, that the number and quality of retention trees are of crucial importance and the continuity of dead wood within the dispersal distance of species must be ensured. If the aim is to support not only common species but also the threatened polypores the goal for retention levels should be more than 20 m^3 ha^{-1} (i.e. the suggested threshold value for occurrence of threatened polypores; Penttilä et al. 2004) to maintain the resources over a time period of several decades. The current levels of tree retention (5 m^3 ha^{-1} in state forests; Heinonen 2006) are clearly not enough to reach this goal. Also, care should be taken not to destroy retained trees in future management practices (Hautala et al. 2004).

3.4 Woodland key habitats can support several polypore species but provide little help for red-listed species

Protection of small-scale habitat types “of special importance for biological diversity” as defined in the Finnish Forest Act aims at saving the ecologically most valuable forest patches within managed forest landscapes. This is believed to be economically cost-efficient because instead of protecting large areas (quantity) as in traditional conservation programs the focus is now in the strictly defined quality of very small areas (mean 0.6 ha; Yrjönen 2004). This quality, however, is defined only by some suggested surrogates of biodiversity – e.g. topographical features, vicinity of water bodies, rich soils – and not by the actual number of species, or presence of red-listed species within the forest patch. Thus, the real biodiversity value of these “woodland key habitats” is poorly known. Furthermore, in the Finnish legislation, natural or old-growth forest as such is not included in the list of key habitat types, which is a clear difference compared to the situation in Sweden and Norway where natural forest is among the most important types of woodland key habitats (e.g. Gustafsson et al. 1999; Sverdrup-Thygeson 2002).

In paper III, the value of woodland key habitats (as defined in the Finnish Forest Act) in maintaining diversity of polypores was recognized: on average, key habitats hosted more species than managed control forests. Of the different habitat types, however, only herb-rich forests were significantly more species-rich than the control forests. Furthermore, although the total number of polypore species at key habitat sites was very high, only few red-listed species were found. This case study of woodland key habitats demonstrates how the total species richness – that can be nicely predicted or explained by habitat heterogeneity (woodland key habitats were very heterogeneous in their tree species composition), or productivity (the most species-rich habitat type was herb-rich forest) – does not necessarily mean richness of rare species (see also Prendergast et al. 1993; Orme et al. 2005). On the other hand, explanation for the absence of rare species can be found by changing the scale of what is a habitat for a polypore: If the habitat is a forest patch (key habitat site), then the diversity or heterogeneity of key habitat sites can be used to explain the total species richness. But if we define the habitat as a dead tree, we realize that these habitats were very homogeneous at least in one respect, the diameter of the dead trees. Most of the dead wood units at the key habitat sites were less than 10 cm in diameter and only few dead trees with a diameter over 30 cm were available. Large dead trees, however, have been found to be essential substrates for many red-listed polypores (Renvall 1995; Berg et al. 2002; Tikkanen et al. 2006) and lack of these substrates, or habitats, means absence of the species dependent on them.

3.5 Short-term effects of logging on polypores are more dramatic than the effects of fire

Almost all differences between natural and managed forests in the boreal can be explained by differences in their disturbance dynamics. In most cases, management for wood production means, for instance, elimination of wildfires, shortened rotation times, lack of dead wood and large deteriorated trees, and homogeneous stand structures (Lindenmayer & McCarthy 2002), and these differences, in turn, are reflected in species composition of the forests. Awareness of these differences has led to adoption of controlled burning as a forest restoration method in Fennoscandian countries, mimicking the most important disturbance of natural forests, wildfires (Christensen 1988; Kouki et al. 2001; Kuuluvainen et al. 2002). The effects of controlled burning on biodiversity, however, have not been comprehensively evaluated (but see Penttilä & Kotiranta 1996; Penttilä 2004; Hyvärinen et al. 2005; Hyvärinen et al. 2006). Furthermore, little is known about the effects of prescribed burning of logged areas on biodiversity.

The short-term effects of fire on polypores depend strongly on whether or not the forest has been logged before the burning (IV). On the time scale of four years, logging – whether followed by prescribed burning or not – changed the species composition of polypore assemblages, increased dominance in assemblages, and increased the overall abundance of polypores but decreased the proportion of red-listed and biodiversity indicator species. None of these changes occurred in the burnt unlogged forests. These results underline the fundamental differences between clear-cutting and wildfire. It is clearly not the fire itself but rather the structural legacies created by fire – amount of dead wood – that largely determines the polypore species composition of a burnt forest site.

4 IMPLICATIONS FOR FOREST MANAGEMENT AND SPECIES CONSERVATION

4.1 Dead wood habitats must be promoted

One cannot get around the general fact that dead wood – its amount and diversity – is the most important factor affecting the species richness and composition of wood-decaying polypore assemblages (Bader et al. 1995; Renvall 1995; Ohlson et al. 1997; Lindblad 1998; Sippola & Renvall 1999; Humphrey et al. 2000; Norden & Paltto 2001; Sippola et al. 2001; Groven et al. 2002; Heilmann-Clausen & Christensen 2004; Penttilä et al. 2004). To gain or maintain diverse local assemblages of polypores, also sources of polypore dispersal are needed (Hallenberg & Küffer 2001; Edman et al. 2004a) in addition to variety of dead wood habitats. Availability of dispersal sources, in turn, is affected by the past continuity of dead wood (Heilmann-Clausen & Christensen 2005) and spatial configuration (including size, fragmentation and isolation) of habitat patches in the landscape (Berglund & Jonsson 2003; Edman et al. 2004b; Berglund & Jonsson 2005; Penttilä et al. 2006).

Thus, in order to maintain or increase the diversity of polypores in managed forests the amount and diversity of dead wood must be promoted. Particularly large dead trees of different tree species and at different decay stages are needed in much larger quantities than they are available in today’s managed forests. In addition to old-growth forests, also young successional forests with abundant dead wood should be available (I, II). In fact, a considerable number of threatened polypore species may have become threatened, not only because of the loss of old-growth forests, but rather because natural young forests with very large amounts of dead wood have disappeared. Increasing the number of retention trees at clear-cut areas (II) would mimic the situation in young natural forest, provided that the oldest and largest trees (representing all tree species) are selected for retention and the total volumes are many times what is seen as a result of current management practises. Controlled burning of the logged area would kill retention trees and accelerate the formation of dead wood, and this practice can be recommended particularly in places where the continuity of dead wood is under threat (IV). Furthermore, the efficiency of woodland key habitats (III) in protection of dead-wood-dependent organisms could be improved by adding a new habitat type in the definition: aggregations of dead trees. These aggregations could be created by any natural disturbance – fire, snow, wind, insect outbreak, pathogens – or by natural senescence of trees, and be located in any type of forest. Leaving these natural legacies in managed forests could be at least as effective as artificial restoration of former managed forests in reserves as a way of promoting the diversity of polypores.

4.2 Polypores as surrogates for conservation of other saproxylic species?

Polypores constitute only a fraction of biodiversity or species richness in forests, and thus, it is clear that the recommendations for protecting (or managing!) the diversity of polypores cannot be applied as such for all other forest-dwelling species. Promoting the diversity of polypores would probably directly promote the diversity of other wood-decomposers as well. In addition, also many others of the estimated number of 5000-7000 saproxylic species in Fennoscandia would benefit, irrespective of their functional groups (Siitonen 2001; Dahlberg & Stokland 2004). There are some obvious differences, however, in the habitat requirements of different species groups utilizing dead wood. Most bark beetles and cavity-nesting birds, for example, favor standing dead trees that have died recently (e.g. Mikusinski & Angelstam 1994; Hyvärinen et al. 2005), contrary to most polypores that are confined (based on the production of fruiting bodies) to fallen trees in advanced stages of decay. Also lichens grow mainly on standing trees, whereas saproxylic bryophytes utilize dead-wood habitats very similar to those of polypores (Söderström 1988; Andersson & Hytteborn 1991; Thor 1998; Johansson & Gustafsson 2001).

The role of polypores at the end part of the wood decomposition process, however, means that where there are suitable habitats available for diverse polypore assemblages, those habitats have already served other species groups that favor earlier decay stages of dead trees. Furthermore, all measures promoting the amount of large dead trees support not only polypores but also most other species associated with dead trees (Kruys et al. 1999; Dahlberg & Stokland 2004) and those species that require large living trees (e.g. nesting sites for birds of prey). Presence of fungi in dead trees also directly facilitates the existence of species dependent on fungal mycelia or fruiting bodies, including other fungi (Niemelä et al. 1995) and many insects and their parasites (Komonen et al. 2000; Komonen 2003; Jonsell & Nordlander 2004). Thus, the measures that promote the diversity of polypores are likely to support also the majority of other species dependent on dead trees or on other structural characteristics typical of old-growth forests. It should be kept in mind, on the other hand, that the measures that are not effective in protection of polypores may still benefit some other groups of species.

4.3 Long-term considerations

All studies assessing the ecological value of the new forestry methods in this thesis (II, III, IV) consider only short time spans. This is understandable given that the forest management methods aimed at enhancing biodiversity are relatively recent in application and their long-term ecological effectiveness is to be seen only as decades pass. This future is difficult to predict because there are several, often conflicting forces acting and interacting simultaneously. The value of woodland key habitats in protecting the diversity of polypores, for example, may increase in future as the trees grow larger and eventually form large-diameter dead wood that is currently lacking from these key habitats (III). On the other hand, the small size of the key habitat sites and their location in fragmented landscape may override this positive development and cause extinction debts (*sensu* Hanski 2000) that will be realized in the future, and the diversity of polypores will actually decrease.

The value of retention trees as well is difficult to predict over more than one rotation period. Although retention trees seem to be suitable habitats even for red-listed species (II), the situation may change if all of the surrounding landscape is subjected to silvicultural management with normal rotation periods. At some point the fruiting bodies growing on retention trees may become the only dispersal sources of polypores within that location, and the small populations face the risk of local extinctions similar to that of polypores in woodland key habitats. Furthermore, if polypore populations are already locally extinct – e.g. many pine-dependent species in southwestern Finland – leaving retention trees of whatever quantity and quality may not bring the species back, simply because there are no dispersal sources. The dispersal ecology of polypores, however, is poorly known (but see Edman et al. 2004a) and this gap in knowledge makes predictions of the future particularly challenging.

Long-term effects of controlled burning of a forest on polypores are also likely to be different from the short-term effects (IV). At clear-cut areas, as soon as the logging residues and cut stumps are completely decomposed, polypores will face a shortage of habitat substrates and their numbers will decline. By that time, on the other hand, some of the retention trees (if there are any) have probably died, particularly if the harvested site has been burnt. Dead, fallen retention trees can provide continuity of dead wood and habitats for polypores as discussed earlier. In unlogged forest, response to controlled burning is much slower than at logged sites (IV), particularly if the fire was not severe. Gradual mortality of trees injured by fire may take several years or even decades and provide an exceptionally good continuity of dead wood which, in turn, will probably result in future increase of polypore diversity (see Penttilä 2004).

Consideration of the temporal dimension can also be extended backwards. One can argue that the results obtained in eastern Finland, particularly those concerning red-listed species, cannot be generalized over areas with longer and more intensive forest utilization history. The differences in the continuity of dead pine trees in my study area compared with areas in the more southern and western parts of Finland, for example, could be seen already in the 1930’s (Kalliola 1966) and this inevitably has affected the local species pools of saproxylics. Thus, it is possible that if the studies had been conducted in more southern parts of Finland, the clear differences in polypore diversity detected between natural and managed forests (I), or between logged and unlogged forests (IV), would not have been so pronounced; but the lack of dispersal sources (caused by breaks in the continuity of large-diameter dead wood and isolation of forest patches) would have confounded the local effects of stand characteristics. Also, the large number of red-listed polypores found on retention aspens (II) is probably related to the exceptionally good continuity of large living and dead aspens in the study area. If the aim, however, is to study stand-level factors that influence red-listed and other rare species and their responses to management treatments, such a study has to take place within the current range of these species; otherwise no differences could be detected. My study areas are among the southernmost of the regions in Finland still supporting populations of most red-listed polypore species with boreal distributions (Kotiranta & Niemelä 1996). Thus, the results of my studies describe the potential effects of different treatments rather than the absolute outcomes that could be expected everywhere. Spatial and temporal factors interact over varying scales in nature and these interactions still require researchers’ attention.

5 CONCLUDING REMARK

In the conservation ecology of saproxylic species, a paradigm shift from emphasizing the importance of old-growth forests into recognizing the role of early successional stages of natural forests as equally important is taking place (Kouki et al. 2001; Martikainen 2001; this thesis). This, however, does not mean that clear-cutting could be regarded as a forestry method that mimics the effects of natural disturbances, but rather that conservation of the remaining patches of old-growth forests or small-scale “woodland key habitats” only is not enough to maintain the diversity of saproxylic species. Instead, focus should be on creating reserves with areas large enough to allow natural disturbances to operate in spatial and temporal scales characteristic of boreal forest ecosystems (Syrjänen et al. 1994; Kuuluvainen 2002; Angelstam & Kuuluvainen 2004). This approach can be complemented by matrix management (Mönkkönen & Reunanen 1999), employing the new biodiversity-oriented forestry methods. But it must be noted, as discussed in this thesis, that the effectiveness of this kind of management as the only method of forest biodiversity conservation is limited. Thus, a shift in a scientific paradigm is not enough but it has to be accompanied by shifts in practical forest management and conservation, if the goal is to fulfill the objectives of the Rio Convention and maintain the full spectrum of biodiversity in our forests.

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APPENDIX. Polypore species included in this thesis.

Complete list of species included in the original articles (I, II, III, IV) in this thesis. Nomenclature for polypores follows Niemelä (2005); those synonym names that have been used in the original articles are also provided, as well as names used in Rassi et al. (2001). Nomenclature of corticiaceous fungi follows mainly Kotiranta (2001). Red List categories are according to Rassi et al. (2001): RE, regionally extinct; EN, endangered; VU, vulnerable; NT, near-threatened. Figures are total numbers of records in the data sets. Note that in IV the total numbers include all records at the same sites in three different years.

Species name	Red-listed	I	II	III	IV	Synonym name
Amylocystis lapponica	VU	2	-	-	6	
Anomoporia bombycina	NT	-	-	2	1	
Anomoporia kamtschatica		5	-	7	14	
Antrodia albobrunnea	NT	11	-	-	6	
Antrodia infirma	VU	1	-	-	3	
Antrodia macra		-	9	5	-	
Antrodia mellita	VU	1	3	-	-	
Antrodia pulvinascens	VU	-	7	-	-	
Antrodia serialis		46	3	11	145	
Antrodia sinuosa		103	-	13	423	
Antrodia xantha		62	-	8	185	
Antrodiella americana	VU	-	-	1	-	
Antrodiella faginea		-	2	12	8	
Antrodiella onychoides		-	-	1	-	
Antrodiella pallescens		8	8	45	16	*Antrodiella semisupina*
Antrodiella parasitica		-	-	-	1	
Antrodiella romellii		-	13	6	5	
Bjerkandera adusta		1	37	29	34	
Bjerkandera fumosa		-	-	4	-	
Byssoporia mollicula		48	-	2	37	*Byssocorticium molliculum*
Ceriporia excelsa		-	-	4	-	
Ceriporia reticulata		-	-	20	-	
Ceriporia viridans		3	26	2	3	
Ceriporiopsis aneirina		-	2	-	-	
Ceriporiopsis resinascens coll.		-	9	13	2	
Cerrena unicolor		4	-	24	110	
Cinereomyces lenis	VU	15	-	-	9	*Skeletocutis lenis*
Cinereomyces lindbladii		2	-	11	25	
Datronia mollis		-	20	17	2	
Dichomitus squalens	NT	-	-	-	35	
Diplomitoporus crustulinus	NT	-	-	-	3	
Diplomitoporus flavescens	VU	-	-	-	1	
Erastia salmonicolor	NT	-	-	-	1	*Hapalopilus salmonicolor*

Species name	**Red-listed**	**I**	**II**	**III**	**IV**	**Synonym name**
Fibroporia gossypium		1	-	1	-	
Fibroporia norrlandica		-	-	2	1	
Fomes fomentarius		41	18	346	697	
Fomitopsis pinicola		67	23	180	552	
Fomitopsis rosea	NT	-	1	-	18	
Funalia trogii	EN	-	3	1	-	
Ganoderma lipsiense		-	7	3	-	
Gelatoporia subvermispora	NT	-	1	-	3	
Gloeophyllum odoratum		-	-	-	1	
Gloeophyllum sepiarium		154	20	7	4041	
Gloeoporus dichrous		-	-	22	27	
Gloeoporus pannocinctus	NT	-	5	5	14	*Gelatoporia pannocincta*
Hapalopilus rutilans		1	-	14	1	
Heterobasidion parviporum		-	-	2	-	
Hyphodontia paradoxa		-	2	3	-	
Hyphodontia radula		-	-	2	2	
Inonotus obliquus		6	-	83	31	
Inonotus radiatus		-	-	9	-	
Inonotus rheades		-	4	1	1	
Irpex lacteus		-	2	1	-	
Ischnoderma benzoinum		2	-	3	1	
Junghuhnia collabens	VU	-	-	-	1	*Steccherinum collabens*
Junghuhnia lacera		-	5	5	-	
Junghuhnia luteoalba		93	-	8	101	
Junghuhnia nitida		-	-	6	-	
Lenzites betulinus		1	4	3	495	
Leptoporus mollis		-	-	-	3	
Meruliopsis taxicola		6	-	3	1	
Oligoporus cerifluus	EN	-	-	-	1	
Oligoporus fragilis		1	-	7	11	
Oligoporus guttulatus	NT	-	-	-	5	*Postia guttulata*
Oligoporus hibernicus	NT	1	-	1	1	*Postia septentrionalis*
Oligoporus lateritius	VU	2	-	-	13	*Postia lateritia*
Oligoporus mappa	RE	-	1	-	-	*Postia mappa*
Oligoporus parvus	NT	-	-	-	5	
Oligoporus ptychogaster		-	-	1	1	
Oligoporus rennyi		7	-	2	8	
Oligoporus sericeomollis		41	-	8	71	
Oligoporus stipticus		1	-	9	4	
Perenniporia tenuis	EN	-	1	-	-	
Phellinus chrysoloma		-	-	2	16	
Phellinus conchatus		1	-	21	1	
Phellinus ferrugineofuscus	NT	3	-	1	37	

Species name	**Red-listed**	**I**	**II**	**III**	**IV**	**Synonym name**
Phellinus igniarius coll.		11	-	398	199	
Phellinus laevigatus		10	-	14	65	
Phellinus lundellii		1	-	9	16	
Phellinus nigrolimitatus		4	-	1	6	
Phellinus pini		7	-	2	72	
Phellinus populicola		-	4	1	12	
Phellinus punctatus		-	-	136	-	
Phellinus tremulae		-	44	21	30	
Phellinus viticola		17	-	12	156	
Physisporinus vitreus		-	-	14	6	
Piptoporus betulinus		24	-	64	171	
Polyporus brumalis		-	-	8	26	
Polyporus ciliatus		8	-	4	14	
Polyporus leptocephalus		-	11	4	1	
Polyporus melanopus		-	-	1	-	
Polyporus tubaeformis		-	-	1	-	
Porpomyces mucidus		1	1	11	4	
Postia alni		-	24	50	17	
Postia caesia		1	-	36	27	
Postia leucomallella		1	-	4	7	
Postia lowei	EN	-	-	-	1	*Oligoporus lowei*
Postia tephroleuca		1	6	16	10	
Protomerulius caryae	VU	-	10	3	14	
Pycnoporellus fulgens		-	-	1	-	
Pycnoporus cinnabarinus		19	2	3	618	
Rhodonia placenta	NT	-	-	-	3	*Postia placenta*
Rigidoporus corticola		-	49	11	29	
Rigidoporus populinus		-	1	19	3	
Sarcoporia polyspora	VU	-	-	1	4	*Parmastomyces mollissimus*
Sistotrema alboluteum	NT	2	2	2	1	
Sistotrema muscicola		2	-	4	4	
Skeletocutis amorpha		39	-	14	248	
Skeletocutis biguttulata		49	-	22	37	
Skeletocutis brevispora	VU	1	-	-	5	
Skeletocutis carneogrisea		1	-	3	2	
Skeletocutis chrysella	NT	-	-	-	1	
Skeletocutis jelicii	EN	-	-	-	2	
Skeletocutis kuehneri		2	-	3	7	
Skeletocutis nivea		-	-	1	-	
Skeletocutis odora	NT	-	3	-	2	
Skeletocutis papyracea		2	-	6	16	
Skeletocutis stellae	VU	2	-	-	2	
Spongiporus undosus		-	2	5	3	*Postia undosa*

Species name	**Red-listed**	**I**	**II**	**III**	**IV**	**Synonym name**
Trametes hirsuta		1	9	14	352	
Trametes ochracea		5	78	68	717	
Trametes pubescens		6	7	3	47	
Trametes velutina		-	-	6	3	
Trametes sp. (young frb)		11	-	-	90	
Trechispora hymenocystis		-	7	141	2	
Trechispora mollusca		-	-	1	5	
Trichaptum abietinum		300	1	176	755	
Trichaptum fuscoviolaceum		119	-	26	318	
Trichaptum pargamenum	NT	3	-	-	10	
Tyromyces chioneus		-	2	7	65	
Corticiaceous fungi (*sensu lato*):						
Aleurodiscus lividocoeruleus		2				
Amphinema byssoides		26				
Amylocorticium cebennense		1				
Asterodon ferruginosus		6				
Asterostroma laxum	NT	14				
Athelia bombacina		13				
Athelia decipiens		3				
Athelia epiphylla		1				
Basidioradulum radula		10				
Boidinia furfuracea		2				
Botryobasidium candicans		5				
Botryobasidium intertextum		1				
Botryobasidium medium	NT	1				
Botryobasidium obtusisporum		1				
Botryobasidium subcoronatum		94				
Botryobasidium vagum		108				
Botryohypochnus isabellinus		9				
Byssomerulius albostramineus		4				
Ceraceomyces borealis		3				
Ceraceomyces cystidiatus	VU	1				
Ceraceomyces eludens		13				
Ceraceomyces microsporus		7				
Ceraceomyces serpens		13				
Ceratobasidium cornigerum		1				
Chaetodermella luna		3				
Chondrostereum purpureum		1				
Conferticium ochraceum		1				
Coniophora arida		12				
Coniophora fusispora		20				
Coniophora olivacea		46				
Coniophora puteana		18				

Species name	**Red-listed**	**I**	**II**	**III**	**IV**	**Synonym name**
Corticium polygonioides		1				
Cristinia helvetica		9				
Cylindrobasidium evolvens		2				
Dacryobolus karstenii		21				
Dacryobolus sudans		2				
Dichostereum boreale		2				
Gloeocystidiellum porosum		1				
Gloiothele citrina		1				
Henningsomyces candidus		1				
Hyphoderma argillaceum		5				
Hyphoderma praetermissum		40				
Hyphoderma puberum		1				
Hyphoderma setigerum		178				
Hyphoderma sibiricum		4				
Hyphodontia abieticola		11				
Hyphodontia alutacea		16				
Hyphodontia alutaria		1				
Hyphodontia aspera		15				
Hyphodontia breviseta		46				
Hyphodontia hastata		16				
Hyphodontia pallidula		5				
Hyphodontia subalutacea		70				
Hyphodontiella multiseptata		1				
Hypochniciellum ovoideum		1				
Hypochnicium eichleri		23				
Hypochnicium multiforme		1				
Hypochnicium punctulatum		6				
Jaapia ochroleuca		2				
Laxitextum bicolor		7				
Leptosporomyces fuscostratus		3				
Leptosporomyces galzinii		7				
Leptosporomyces septentrionalis		4				
Leucogyrophana mollusca		6				
Leucogyrophana romellii		53				
Leucogyrophana sororia		4				
Megalocystidium leucoxanthum		1				
Metulodontia nivea	NT	9				
Mucronella bresadolae		1				
Mucronella calva		2				
Mucronella flava		2				
Odonticium romellii	NT	10				
Peniophora incarnata		2				
Peniophora pithya		71				

Species name	**Red-listed**	**I**	**II**	**III**	**IV**	**Synonym name**
Phanerochaete laevis		37				
Phanerochaete magnoliae		2				
Phanerochaete sanguinea		147				
Phanerochaete sordida		115				
Phanerochaete velutina		18				
Phlebia cornea	NT	4				
Phlebia cretacea		12				
Phlebia firma	NT	2				
Phlebia fuscoatra		7				
Phlebia gigantea		49				
Phlebia lilascens		1				
Phlebia livida		19				
Phlebia radiata		3				
Phlebia rufa		1				
Phlebia segregata		2				
Phlebia serialis	NT	1				
Phlebia tremellosa		6				
Phlebia tristis		1				
Phlebiella allantospora		1				
Phlebiella borealis		1				
Phlebiella pseudotsugae		7				
Phlebiella sulphurea		854				
Piloderma byssinum		19				
Piloderma fallax		213				
Pseudomerulius aureus		6				
Resinicium bicolor		31				
Resinicium furfuraceum		639				
Scytinostroma praestans	NT	1				
Serpula himantioides		24				
Sistotrema brinkmannii		5				
Sistotrema octosporum		23				
Sistotrema raduloides	NT	1				
Sistotremastrum suecicum		146				
Sphaerobasidium minutum		2				
Steccherinum ochraceum		1				
Stereum hirsutum		14				
Stereum rugosum		4				
Stereum sanguinolentum		139				
Stereum subtomentosum		1				
Thanatephorus cucumeris		1				
Thanatephorus fusisporus		7				
Thelephora terrestris		147				
Trechispora byssinella		3				

Species name	Red-listed	I	II	III	IV	Synonym name
Trechispora cohaerens		5				
Trechispora farinacea		55				
Trechispora kavinioides		2				
Trechispora lunata		6				
Trechispora nivea		2				
Trechispora subsphaerospora		2				
Trechispora tenuicula		1				
Tubulicrinis borealis		1				
Tubulicrinis calothrix		3				
Tubulicrinis glebulosus		6				
Tubulicrinis medius		1				
Tubulicrinis strangulatus		4				
Tubulicrinis subulatus		14				
Tylospora fibrillosa		1				
Vararia investiens		10				
Veluticeps abietina		3				