**Dissertationes Forestales 279**

# The structure of macrofungal assemblages in boreal forests, with particular reference to the effect of fire on Basidiomycota and Ascomycota

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Academic dissertation

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# ABSTRACT

The majority of forests in Finland have been subject to intensive clear-cutting and thinning, and peatlands have been extensively ditched and fertilized. Such changes have modified forest environments but the effects of these changes on macrofungi are still unclear. This thesis examines macrofungal communities in boreal forests and peatlands, with particular focus on the effects of wildfire, prescribed burning and tree retention (timber harvest intensity) on ectomycorrhizal (ECM) and saprotrophic (SM) macrofungi (Basidiomycota and Ascomycota). The thesis is based on empirical field data, which includes over 550 species and a monitoring period of up to 12 years.

Fertile forests had more diverse ECM and SM assemblages than the dry and semi-dry forests. Non-ditched pine bogs had less macrofungi than drained spruce mires, pine mires and pine bogs. Rare and Red-listed agarics and aphyllophoroid wood-associated macrofungal species were rare in managed forests.

In general, wildfire increased the richness and sporocarp production of several SM species and also modified assemblage composition. ECM diversity was greatest in the mild and intermediate fire sites where it was three-fold higher than the high-severity fire sites. The succession of fire-associated pyrophilous species in burned humus was rapid.

Prescribed burning and harvest intensity had a major influence on macrofungal populations. However, these effects were strongly dependent on the functional group. Clear-cut areas had an overall adverse effect on macrofungi; ECM species in particular disappeared after clear-cutting. Several SM species occurred exclusively on burned areas, and retention areas had a slight positive effect on macrofungi, including ECM species.

My results show that macrofungal assemblages are diverse and vary systematically in forest and peatland site types. Intensive forest management has mostly negative effects on macrofungi, including edible mushroom species. Prescribed fire in the forest landscape and a reduction in harvest intensity can be used to maintain fungal assemblage diversity in managed forests.

**Keywords**: Wildfire, post-fire, fire severity, disturbance, fungi, forest management

# KIITOKSET / ACKNOWLEDGEMENTS

Kesällä 1966 peltopyy oli muninut pesäkuoppaan kaksitoista ruskeaa munaa vanhan heinittyneen peltotien reunalle. Toisella puolella ojaa oli ojitettu rämelaikku, jossa rämemännyt kasvoivat hyvin. Tupasvillamättäiden reunamilla kasvoi ruskeita sieniä, ne olivat tuntemattomia madonlakkeja. Seuraavana keväänä lumet sulivat pelloilta, tuli ”paisunta” ja valokuvasin laulujoutsenia tulvapelloilla. Tulvivan peltolakeuden taustalla näkyi Lakeuden Risti. Kyrönjoen sivujoen, Seinäjoen varrella sadat harmaat ladot täplittivät maisemaa. Kesä- ja talviaikaan kuvasin peltopyitä, jotka olivat suojassa pedoilta ladoissa ja latojen sisältä löytyi myös jyviä syötäväksi. Latojen ympärillä kasvoi punertavia ja kellertäviä sieniä, niitä ei kukaan tuntenut, nekin olivat madonlakkeja. Peltolakeuksien linnut ja kasvit opin tuntemaan, mutta itiöemien tunnistaminen ja sienirihmastojen merkitys metsän ekosysteemissä oli lukioaikana lähes tuntematonta aluetta.

Eteläpohjalaiseen tapaan kotonani ruokasieniä ei syöty. Käkisalmella syntynyt anoppini Kaarina Korpela tunsi karjalaisena muutamia ruokasieniä, kävimme sieniretkillä ja opin syömään herkkutattipiirakkaa. Kaarinalle kiitos sieniruuista, joiden makuihin totuin nopeasti. Opiskeluaikana ja myöhemmin metsien monikäytön erikoistutkijana opin näkemään ruokasienten ja metsien ekosysteemipalveluiden merkityksen ihmisen taloudessa.

Aloitin opintoni 1970-luvun alkupuolella Helsingin yliopiston Kasvitieteen laitoksella, jossa opettajat olivat päteviä ja kannustavia. Kasvitieteen laitoksen kolmannessa kerroksessa tapasin myös eteviä sienitutkijoita. Heidän opastuksellaan syntyi palava halu oppia lisää sienten merkityksestä luonnon ekosysteemeissä. Haluan osoittaa kiitokseni erityisesti Helsingin yliopiston professoreille Leena Hämet-Ahti, Teuvo Ahti ja Rauno Ruuhijärvi, tohtoreille Harri Harmaja, Veikko Hintikka, Marja Härkönen ja tohtori h.c. Mauri Korhonen sekä Oulun yliopiston tohtori Esteri Ohenojalle.

Kansainvälisissä sienikongresseissa ja monilla sienitieteellisillä tutkimusmatkoilla olen tavannut maailman johtavia sienitutkijoita, jotka ovat jääneet pysyvästi mieleeni. Kiinnostukseni on noista vuosista kantanut eteenpäin, kasvanut ja laajentunut, nyt jo yli 40 vuoden ajan. Väitöstutkimukseni on olennainen päätös sienten monimuotoiseen maailmaan. Mikään työ ei kuitenkaan synny itsestään, ja matkani varrella lukuisat ihmiset ovat eri tavoin auttaneet minua saavuttamaan tämän akateemisen päämäärän.

Väitöskirjani ohjaaja, professori Jari Kouki on aikaansa säästämättä kannustanut ja ohjannut väitöskirjani valmistumista. Jarin kanssa olemme miettineet, pohtineet ja työstäneet suurimman osan väitöskirjan julkaisuista. Yhteistyömme on ollut tiivistä ja opettavaista, todellinen matka tieteelliseen ajatteluun. Erityisesti Jarin 1990-luvun lopulla käynnistämä laaja metsäpalotutkimus – FIRE-hanke – oli lähtölaukaus myös meidän yhteistyöllemme noin 20 vuotta sitten. Kollegani MMT Timo Domisch osallistui väitöskirjan kolmannen osatyön aineistojen analyysin, ja hänen kykynsä käsitellä laajoja sieniaineistoja oli erityisen ansiokasta ja minulle opettavaista. The English language was revised by Dr. David Wilson, my sincere thanks belong to him. Kiitän väitöskirjani esitarkastajia, professori emeritus Pekka Niemelää ja erikoistutkija, FT Heikki Kotirantaa.

Vuonna 1981 alkoi sienitutkimus osana valtakunnan metsien inventointia pysyvillä koealoilla Pohjois-Karjalassa. FL Juha-Pekka Hotasen ja FM Hannu Nousiaisen kanssa keräsimme koeruuduilta suuren aineiston puista ja pensaista, kenttä- ja pohjakerroksen kasvilajeista ja sienistä, jotka sittemmin päätyivät väitöskirjan ensimmäiseen osajulkaisuun. Yhteiset hetket maastossa ja työpäivien jälkeen Metsähallituksen Kukkarolammen, Palkinvaaran ja

Palovaaran metsäkämpissä sekä Hirvivaaran talossa ja saunoissa eivät unohdu koskaan. Myöhempinä vuosina heidän ystävyytensä on ollut merkittävää. Kiitos Juha-Pekalle ja Hannulle.

Metsäntutkimuslaitoksen (Metla) Metsämarja- ja sieniprojekti sekä Metsien monikäytön tutkimusohjelma tarjosivat sieniaineistojen keräysvaiheessa erinomaisen tutkimus- ja työympäristön. Erityiskiitos Metlan suontutkimusosaston johtajalle, prosessori Eero Paavilaiselle. Myöhemmin Metla-talon ja Luonnonvarakeskuksen (Luke) tilat laboratorioineen olivat erinomaisia sienilajien määritystyössä. Kiitos Metlan Joensuun tutkimusaseman johtajalle, MMT Jari Parviaiselle. Kiitos Luken Biotalous ja ympäristö -yksikön johtajalle, ETT Sari Forsman-Huggille ja Virkistys ja luontoarvot -ryhmän ryhmäpäällikkö, ETM Jaana Kotrolle mahdollisuudesta keskittyä täysipäiväisesti väitöskirjatyön viimeistelyyn hiljaisen työn alueella Metla-talossa.

Kitsin metsäpaloalue ja FIRE-tutkimusalue muodostuivat keskeisiksi tutkimuskohteiksi 1990-luvulla ja 2000-luvun alkuvuosina. Metsähallitus rauhoitti Kitsin metsäpaloalueen luonnon laboratorioksi ja toteutti FIRE-alueen kulotukset ja hakkuut. Kiitos Metsähallitukselle hyvästä yhteistyöstä ja tutkimuspaikoista, jotka sijaitsivat kaukana keskustaajamista. Koeruuduilta kerättiin ahkerasti sieniä, mutta nautittiin myös luonnon hiljaisuudesta ja nuotiokahveista.

Kitsin metsäpaloalueella maiseman yleisväri oli musta ja pohjantikoilla oli runsas pesintä tutkimukseni ensimmäisinä vuosina. Tuolloin nokilakkien ja palohelokoitten tuhannet itiöemät palaneella humuksella jäivät mieleen sekä nokinen työympäristö. Pystyyn palaneitten, kuolleitten puitten metsä on vuosien aikana muuttunut vihreitten mäntyjen ja maassa makaavien harmaitten kelojen hallitsemaksi maisema-alueeksi.

Maastotöissä monet henkilöt ovat keränneet kanssani suuren määrän erilaisia sieniä. Jokaiselle kerätylle sienilajille on määritetty latinankielinen nimi. Sienet eivät olleet enää tuntemattomia madonlakkeja. Anki Geddala, Suvi Hirvonen, Hanna Keski-Karhu, Markku Kanerva, Esko Kauppinen, Seija Sulonen, Markku Tiainen, Heimo Tynkkynen ja Tapio Ylimartimo, kiitos jokaiselle arvokkaasta työpanoksesta sienten keräysretkillä. FT Markku Kirsi oli merkittävänä apuna eräiden sienilajien määrittämisessä.

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Joensuussa ja Savonlinnan Savonrannassa, Savonselän rannalla 5.5.2019.

Kauko Salo

Kauko Salo

## Sienet

*Pitkien sateitten jälkeen*
*syksyn keltaisten lehtien lomista*
*puhkeavat sienet*
*omituisesti tuoksuvina*
*kasvaen kylmiksi ja lihaviksi*
*kuolleitten kasvien ja eläinten ruumiista.*

*Haperoiden lakit ovat kuin himmeästikiiltävää,*
*punaista tai kellertävää porsliinia.*
*Haapasienet nousevat maasta*
*hauraina ja naurettavan pieninä*
*muistuttaen kuolleen lapsen harmahtavia korvalehtiä.*

*Keltasienet hymyilevät kuivina ja iloisina,*
*siroina ja keltaisina kuin voi.*
*Yksinäisinä, suurina ja ilkeinä*
*loistavat kauniitten kärpässienten*
*punaiset, valkopilkkuiset lakit*
*hohtavanvalkoisten jalkainsa kannattamina.*
*Tatit komeilevat suuruudellaan,*
*ruskeankeltaisina, kömpelöinä ja tyhminä.*
*Imevät itseensä paljon kosteutta ja matoja*
*ja putoavat lopulta ilettäviksi, limaisiksi kasoiksi.*

*Mutta tummanruskean, kiinteän herkkutatin*
*tahtoisi syödä juuri maasta poimittuna,*
*vielä mullalle tuoksuavana.*

Katri Vala 1924

# LIST OF ORIGINAL ARTICLES

The thesis is based on the following journal articles or manuscripts, which are referred to in the text by the Roman numerals **I-IV**:

**I** Salo, K. (1993). The composition and structure of macrofungus communities in boreal upland type forests and peatlands in North Karelia, Finland. Karstenia 33: 61–99. https://doi.org/10.29203/ka.1993.299

**II** Salo, K., Kouki, J. (2018). Severity of forest wildfire had a major influence on early successional ectomycorrhizal macrofungi assemblages, including edible mushrooms. Forest Ecology and Management 415-416: 70–84. https://doi.org/10.1016/j.foreco.2017.12.044

**III** Salo, K., Domisch, T., Kouki, J. (2019). Forest wildfire and 12 years postfire-disturbance succession of saprotrophic macrofungi (Basidiomycota, Ascomycota). Submitted to Forest Ecology and Management.

**IV** Kouki, J., Salo, K. (2019). Forest disturbances modify functional groups of fungi in young successional forests – clear-cut and fire lead to different fungal assemblages. Manuscript.

Contribution of Kauko Salo to the studies included in this thesis was as follows:

Study **I**: Original idea, data sampling and macrofungi identification, data analyses and manuscript writing.

Study **II**: Original idea, data sampling and macrofungi identification. Contributed to data analyses and wrote the manuscript together with co-author.

Study **III**: Original idea, data sampling and macrofungi identification. Contributed to data analyses and wrote the manuscript together with the co-authors.

Study **IV**: Original idea with the co-author, data sampling and macrofungi identification and wrote the manuscript together with the co-author.

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# ABBREVIATIONS

Abbreviations in this thesis and an explanation of the fungal groups are explained in more detail in the original scientific publications.

| | |
|---|---|
| 7NFI | 7th Finnish National Forest Inventory, a network of permanent sample plots in North Karelia. |
| AWAM | Aphyllophoroid wood-associated macrofungi. |
| BM | Biotrophic macrofungi, fungi that form a relationship between algae and fungi, living in mutual symbiosis with mycorrhizae. |
| CWD | Coarse woody debris. |
| DeMT | *Deschampsia-Myrtillus* Type, mesic forest site type. |
| DCA | Detrended correspondence analysis, statistical ordination method. |
| ECM | Ectomycorrhizal macrofungi, a symbiotic connection between the mycelium of a fungus and the roots of a plant. |
| ECT | *Empetrum-Calluna* Type, dry forest site type. |
| EVT | *Empetrum-Vaccinium* Type, semi-dry forest site type. |
| FWD | Fine woody debris. |
| FIRE | Large forest experiment area in eastern Finland, 16 sites covered each of 3-5 ha in this study. More detailed information: http://forest.uef.fi/jarikouki/project_fire.htm |
| GOMT | *Geranium-Oxalis-Myrtillus* Type, rich forest site type. |
| HOT, HOT-DRY, MEDIUM, MILD, | fire severity classes from the most severe to least ones, based on immediate effects that fire had on trees and soil. Also names used of burned sites in KITSI. |
| HS | Humus saprophytes living in fresh or burned humus. |
| IR | True dwarf shrub pine bog. |
| IS | Indicator species, statistical method used to analyze IS in burned and unburned sites. |
| KITSI | Kitsi forest fire area in North Karelia, burned 7 June 1992, the size of the burned area covering 143 ha. |
| LkN | Ombrotrophic small sedge bog. |
| NMDS | Non-metric multidimensional scaling, statistical analysis on species composition and community structure. |
| PM | Parasitic macrofungi, living on plants or on other macrofungi, cause harms or kill the host. |
| PsR | *Cares globularis* pine mire. |
| RaR | *Sphagnum fuscum* pine bog. |
| SaM | Saprophyte macrofungi, on substrates other than wood, decomposing dead organic matter or living in mineral soil. |
| SM | Saprotrophic macrofungi, all macrofungi that decompose dead organic matter. |
| SOM | Soil organic matter. |
| TR | *Eriophorum vaginatum* pine bog. |
| TWINSPAN | Two-way indicator species analysis. Statistical classification method of macrofungi. |
| VMT | *Vaccinium-Myrtillus* Type, mesic forest site type. |
| WAM | Wood-associated macrofungi. |

# 1. INTRODUCTION

## 1.1 Kingdom Fungi

Nowadays, fungi are classified as the third kingdom (in addition to the traditional kingdoms of Animalia and Plantae). It is highly diverse kingdom with 144,000 species named and classified to date (Hibbet et al. 2007).

However, the vast majority of fungal species are probably unknown to science, and the total number of species on Earth is estimated at between 2.2 and 3.8 million (Hawksworth and Lucking 2017). A large number of new macrofungal species have been recognized in recent years following the development of DNA-based techniques. For example, a total of 2189 new species of fungi were described in 2017, which included 1481 species in the phylum Ascomycota, and 684 in Basidiomycota (Hibbet et al. 2007).

My thesis includes macrofungi from Basidiomycota and Ascomycota. In Finland, boletoid and agaricoid fungi include 2,082 species or lower taxa (von Bonsdorff et al. 2019), and 991 species of Aphyllophoroid fungi of which 251 species are polypores (Kotiranta et al. 2019). In Finland, there are more than 200 edible mushroom species (von Bonsdorff et al. 2013), many of which are also used commercially.

The number of macrofungi in this thesis represent about 20 % of boletoid and agaricoid macrofungi found in Finland, and an even higher proportion of macrofungi living in semi-dry (*Vaccinium-vitis-idaea* forest site type) and mesic (*V. myrtillus* forest site type) pine and spruce dominated forests.

## 1.2. Ecological research of macrofungal communities

Macrofungal communities have been investigated since the early 1900s. One of the first sociological and ecological macrofungal yield studies was carried out in Germany by Haas (1932) followed by Friedrich (1936) and Leischner-Siska (1939). Höfler (1937) counted the number of sporocarps and weighed fresh macrofungi in a beech forest in Austria. He understood that fungal communities were their own ecological unit and also plant communities. Later, several taxonomic and yield studies were published from European sites, e.g. Guminska (1966) in Poland, Kalamees (1968) in Estonia, Darimont (1973) in Belgium, and Barkman (1976) in the Netherlands. Kalamees (1980) studied the taxonomy and trophic groups of macrofungi during the different seasons of the year.

Later, Kardell et al. (1980) carried out a macrofungal yield study based on the National Forest Inventory (NFI) in Sweden and, since then, several studies have investigated the effects of silvicultural actions on fungal yield (e.g. Wästerlund and Ingelög 1981; Kardell 1984; Kardell and Eriksson 1987). In Norway, and Mehus (1986) studied the macrofungi that live in different forest site types. In the 1980s, forest damage in conifers caused by acid rain was observed in Central Europe (Blaschke 1988) and the effects of air pollutants on mycorrhizal macrofungi were studied in the Netherlands by Jansen and van Dobben (1987), Jansen and Dighton (1990) and Arnolds (1991). Moreover, ectomycorrhizal (ECM) species are also sensitive to nitrogen (N) fertilization (Markkola et al. 1995) and forest regeneration methods (Hanger 1995, Kåren 1997).

One of the first ecological and phenological studies of macrofungi was carried out by Thesleff (1920) in Vyborg, Finland. Later, Rautavaara (1947) made a detailed account of macrofungi based on transect surveys. Hintikka (1988) studied macrofungal composition in pine forests of different ages, and Ohenoja and Koistinen (1984) studied the yields of edible mushrooms in 15 localities in northern Finland. Ohenoja (1993) studied the effects of weather on macrofungi, and Väre et al. (1996) quantified macrofungal yields in pine forests in northern Finland.

Mycological studies also extended to peatlands when Lange (1948) studied the ecology of agarics in Maglemose mire in Denmark, Favre (1948) in bogs in Switzerland, Kotlaba and Kubicka (1960) in (the current) Czech Republic, Kreisel (1954) and Einhellinger (1976, 1977, 1982) in Germany. Kalamees (1982) clarified the composition and seasonal dynamics of macrofungi in Estonian peatlands. Macrofungal studies of Finnish peatlands were rare for a long time until Veijalainen (1974) studied macrofungal production in drained peatlands, Salo (1979) investigated macrofungal species and yield in drained and fertilized pine bogs, and Salonen and Saari (1990) explored macrofungal communities in pristine mires.

In the 1990s and early 2000s, macrofungal studies were directed to ECM species diversity, sporocarp production, and community structure (Visser 1995; Dahlberg et al. 1997; Jonsson et al. 1999; Bonet et al. 2004). At the same time, interest in wood-associated macrofungi (WAM) (wood-inhabiting wood-decaying, wood-fungi, wood-decomposing and wood-rotting fungi were also used) was stimulated in Finland (e.g. Renvall 1995; Sippola and Renvall 1999; Siitonen et al. 2000; Penttilä et al. 2004; Junninen et al. 2006, Hottola and Siitonen 2008; Halme et al. 2009), Sweden (Bader et al. 1995; Berglund et al. 2005), Denmark (Heilmann-Clausen and Cristensen 2004), and Germany (Müller et al. 2007). Dead-wood-associated aphyllophoroid fungi have been of interest in conservation biology (reviewed by Junninen and Komonen 2011) and in an assessment of the ecological effects of disturbance-based restoration (e.g. Pasanen 2017).

Interest in the effects of forest wildfires on ECM communities started in the boreal forests in Sweden (Dahlberg et al. 2001; Dahlberg 2002), expanded to Mediterranean forests in Spain (Martin-Pinto et al. 2006; Vasques Gassibe et al. 2011; Mediavilla et al. 2014) and onto Argentina, and included the long term effects on ECM and soil properties (Longo et al. 2011). In the 1990s and the early years of the 2000s, the effect of prescribed burning on ECM (Stendell et al. 1999) and WAM (Penttilä and Kotiranta 1996) was also of considerable interest.

During the last decade, studies have focused on the impact of restoration and prescribed burning; mainly on polypores (Junninen et al. 2008; Olsson and Jonsson 2010; Penttilä et al. 2013; Suominen et al. 2015, 2018). The effects of climate change (Heilmann-Clausen and Lassöe 2012; Boddy et al. 2014) and forest management (Juutilainen et al. 2014) have received increased attention, although studies on fire and saprophyte macrofungi (SaM) assemblages on substrates other than wood are still scarce.

However, the effects of fire on fungi have attracted attention for over a century. For example, Seaver (1909) was the first investigator to focus on a special group of fungi that are adapted to fire. He called them pyrophilous fungi; a name derived from the genus *Pyronema* in his article, Seaver wrote, “The genus *Pyronema* includes several species, which, as the name implies, commonly inhabit burnt places.”

Lange (1944) presented a short report of the fungi found on a number of burns, using the frequency of the species on the burns as a quantitative measure. The first paper concerning the effects of fire on macrofungal communities was by Moser (1949), written in German. He grouped the macrofungi into five groups in burned areas: 1. Anthracophilous (Anthracobionte) macrofungi which were described as obligate fireplace fungi. 2. Anthracophilous (Anthrakophile) macrofungi are favored by fire. 3. Anthracoxenous (Anthrakoxene) macrofungi which appear accidentally in fire areas. 4. Anthracophobe (Anthrakophobe) macrofungi suffer from fire and sporocarp formation is prevented in burnt areas.

Lange (1944) used the term “charcoal-loving” for fungi of burned ground. Later, Pirk (1950) and Ebert (1958) studied macrofungi in fireplaces and Petersen (1970) analyzed the development and seasonal variation of the macrofungi in fireplace burns.

The classification of Moser (1949) did not gain popularity and, nowadays, fire-associated species are mainly called pyrophilous species, although Pirk (1950) did describe carbophilous macrofungal communities (carbophile Pilzassociation), while Petersen (1970) used the term “fireplace fungi”, described successional patterns and divided species into groups according to the time of occurrence following fire (Petersen 1971). Moreover, Wicklow (1975) used both the terms “carbonicole fungi” and “charcoal-loving fungi”.

## 1.3 Fires and their ecological effects in forests

Wildfires are the most common natural disturbance in boreal forests (Goldammer and Furyaev 1996), and this also applies historically to boreal forests in Fennoscandia (Zackrisson 1977, Schimmel and Granström 1996). Nowadays, the annually burned area is very small in Fennoscandia, while 1 % of boreal forests are generally burned every year (Gauthier et al. 2015). Large wildfires have huge importance for the carbon (C) and N cycles (Flannigan et al. 2009).

In the Fennoscandian area, forests have historically burned at intervals of 50–200 years, depending on the prevailing weather conditions and site type (Zackrisson 1977; Wallenius et al. 2004; Granström and Niklasson 2008; Schimmel and Granström 2011). However, fire intervals can be up to a thousand years in northern Finland (Wallenius et al. 2005). Only 50 % of all wildfires in Finland are estimated to be severe crown fires (Pitkänen and Huttunen 1999). At the present time, forest fires rarely occur in Finland and are small in size; for example, there were 1,504 fires but only 469 hectares were burned in the whole country in 2013 (Finnish Statistical Yearbook of Forestry 2014a).

Wildfires are not homogenous; each fire typically produces a range of severity (from high to low) that leads to large heterogeneity within a burned site (e.g. Kafka et al. 2001). In boreal forests, wildfires create or affect patch mosaics, tree stand structure and soil dynamics (Zackrisson 1977; Bergeron 1991). According to Lehtonen and Huttunen (1997) only some moist forests remain as refugia outside forest fires.

Spatial effects and the small-scale variation of fire is obvious in soil organic matter (SOM) and related soil C stocks and N balance (Čugunovs et al. 2017; Palviainen et al. 2017). In addition, fire typically reduces species richness and diversity of soil microorganisms (bacteria, fungi and Archaea) and soil micro- and meso-fauna (e.g. Protozoa, nematodes, microarthropods) (Pressler et al. 2019).

Forest fires affect the quantity and quality of SOM and soil microbes (Pietikäinen and Fritze 1995; Köster et al. 2014). There is an increase in soil temperature and a decrease in moisture conditions after fire because dry charred humus surfaces absorb solar radiation effectively (Viro 1969; Certini 2005).

Two fungal meta-analysis studies were recently published where the effect of fire on soil biota microorganisms and mesofauna was investigated and fungal species richness response to fire was examined. Fungal species richness and mycorrhizal colonization were found to be reduced after fire but soil fungi are flexible and are able to rapidly recolonize post-fire areas (Dove and Hart 2017). In 131 empirical studies, fire was shown to have a very negative effect on soil microorganisms, and little change was observed in soil microbe populations 10 years post-fire (Pressler et al. 2019).

Typically, it is only the severe fires that kill all the trees. Tree and plant mortality create a large volume of dead organic matter (Kouki et al. 2001, Junninen et al. 2006) and provide resources for a diverse ecological group of animals, plants and fungi that can live on dead wood substrates (Siitonen 2001).

After severe fires, the understory vegetation burns to ash and nutrients are released, the mineral soil can be exposed, and these sites are suitable for the seeds of conifers to germinate and for new plants to grow (Schimmel and Granström 1996, Ruokolainen and Salo 2006). Post-fire forests also create new habitats and resources for many polypore fungi (Penttilä et al. 2013; Suominen et al. 2015, 2018). Fires are also considered a dominant factor in determining the dynamics and diversity of ECM (Taudiere et al. 2017) and SM communities, and high severity fires play an important role in the succession of ECM, pyrophilous saprophytes and aphyllophoroid wood-associated macrofungi (AWAM).

Taudiere et al. (2017) recently reviewed 73 field studies that examined the effects of forest fires on ECM symbioses. The studies were located in boreal (10), Mediterranean (20), temperate (35) and tropical ecosystems (2), and 44 of the publications focused on *Pinus*-dominated ecosystems. Moreover, 20 publications examined the effects of fire (13 wildfires and 7 prescribed burnings) on fungal species richness (Taudiere et al. 2017). The results in regard to the effects of fire on ECM species were ambiguous and included both positive and negative effects.

Studies have pointed out that wildfires in boreal forests have adverse effects on ECM macrofungal diversity (Jonsson et al. 1999; Dahlberg 2002). In addition, the short-term effects on wood-inhabiting polypores, including Red-listed species, is often negative (Junninen et al. 2008; Penttilä et al. 2013; Suominen et al. 2015). Prescribed burnings, on the other hand, create dead woody material that includes many decay stages of coarse woody debris (CWD), which are suitable for numerous polypore and aphyllophoroid species (Penttilä and Kotiranta 1996; Penttilä et al. 2013).

In temperate forests, fires are often severe and their effects on ECM species and sporocarp production have also been shown to be negative in pine forests in Spain (Torres and Honrubia 1997; Martin-Pinto et al. 2006; Vasquez Gassibe et al. 2011; Hernandez-Rodriguez et al. 2013; Mediavilla et al. 2014) and in temperate forests in Lithuania (Motiejūnaitė et al. 2014). Increasing interest has focused on forest fires and macrofungi outside of Europe, for example in Indonesia (Mardji 2014), and on the importance of mushrooms as a nutritious food for people living in rural areas in Ethiopia (Dejene et al. 2017).

In the future, it is expected that fire frequency will increase as a result of climate change (Bond-Lamberty et al. 2006; Flannigan et al. 2009; Kilpeläinen et al. 2010), with consequent changes in disturbance patterns in forests (Seidl et al. 2017). Climate change can be expected to affect ECM communities by changing species composition and the structure of the tree stand (Büntgen et al. 2011; Boddy et al. 2014).

## 1.4 The effects of forest management on macrofungi

Intensive forest management profoundly modifies forest ecosystems, and these changes can also have a major impact on macrofungi. For instance, ECM species are associated with living trees and, thus, clear-cutting is expected to have a strong effect on ECM species. Intensive forest management also reduces the amount of large, dead trees, which may influence wood-associated fungi (Junninen and Komonen 2011). On the other hand, harvesting may increase the amount of small-diameter woody debris (branches, needles etc.) and, thus, have positive effects on the species that are able to use these resources.

In Finland, the mean volume of decaying and dead trees on forest land (i.e. forest available wood supply containing mainly managed forests) was 4.8 $m^3$ $ha^{-1}$ in the 9th NFI (1996–2003) but only 4.3 $m^3$ $ha^{-1}$ in the 12th NFI (2009–2013) (Finnish Statistical Yearbook of Forestry 2014b). The corresponding mean values for legally protected forest areas (nature and national parks, nature reserves) were 20.0 $m^3$ $ha^{-1}$ in the 9th NFI and 17.9 $m^3$ $ha^{-1}$ in the 12th NFI (Korhonen et al. 2017). The mean volume of decaying and dead trees was 4–5 times higher in the national parks and nature reserves than in managed forests but were still below the levels typically observed in natural forests. The volume of dead wood in natural forests varies according to productivity and location and is about 20–130 $m^3$ $ha^{-1}$ (Kouki et al. 2001, Siitonen et al. 2001).

Large decaying logs (diameter > 20 cm) on the ground at the substrate scale have been shown to be the most important factor explaining WAM species richness, and the occurrence of rare polypore species was strongly influenced by 20–40 $m^3$ $ha^{-1}$ of dead wood at the stand scale (Junninen and Komonen 2011). Thus, the overall effect of intensive forest management on fungi, and on wood-associated fungi especially, is most often negative (e.g. Junninen et al. 2006; Müller et al. 2007a, b).

### 1.5 Aims of the thesis

My thesis is divided into two; whereby the first part focuses on macrofungal species richness and communities in different boreal forests and peatland site types (**I**). In the second part, I examine the effects of forest wildfire on macrofungal richness, community composition and succession 12 years after wildfire (**II**, **III**) and three years after prescribed burnings (**IV**).

The main research questions asked in this thesis were:

- Does ECM, SM and parasitic macrofungi (PM) species richness and their composition differ from each other in managed mineral soil forests (including mixed and forest site types) and peatland site types? (**I**)
- How does forest management affect the populations of ECM, SM, AWAM and edible mushroom species? (**I**)
- How is macrofungal species richness and community composition affected by (a) wildfire and (b) prescribed burning and retention? (**II**, **III**, **IV**)
- What is the role of fire severity on macrofungi assemblages? (**II**, **III**)
- How does ECM species succession differ from pyrophilous species succession in burned humus and from AWAM and other macrofungal species succession in burned wood in different fire severity classes? (**II**, **III**)
- How are edible mushrooms affected by forest fires? (**II**, **III**, **IV**)

## 2. MATERIALS AND METHODS

### 2.1 Study sites and experimental design

The total number of identified macrofungal species or species groups (Basidiomycota, Ascomycota), main functional groups and their percentage values, total number of sporocarps and total yield is shown in Table 1 (**I**, **II**, **III**, **IV**). Examples of the macrofungi included in this study are shown on Figure 1.

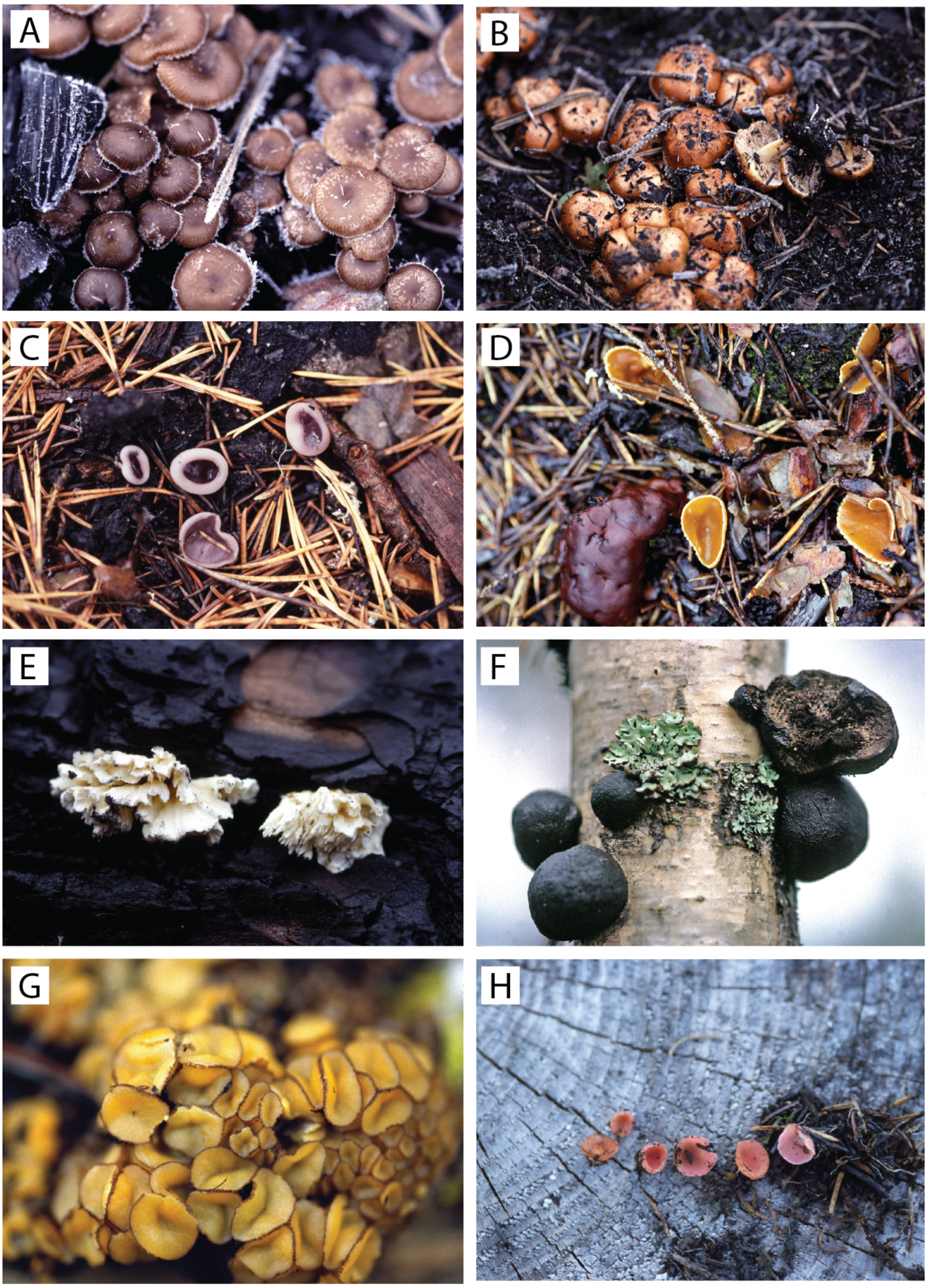

**Figure 1.** Species of macrofungi included in this study. All examples are on burned substrates: A) *Myxomphalia maura* (agaric on humus), B) *Pholiota highlandensis* (agaric on humus), C) *Peziza violacea* (ascomycete on humus), D) *Rhizina undulata* (parasitic species, left) and *Geopyxis carbonaria* (biotrophic species, right), E) *Irpicodon pendulus* (wood-associated hydnaceous species), F) *Daldinia concentrica* (wood-associated ascomycete), G) *Antracobia macrocystis* (ascomycete on humus), H) *Rhodotarzetta rosea* (ascomycete on humus; sporocarps placed on a stump for photographing). Photos: Kauko Salo.

**Table 1.** Total number of identified macrofungal species or species groups, main functional group and their percentage value in parentheses, total number of sporocarps and total yield (g in fresh weight) in studies **I**, **II**, **III** and **IV**. For abbreviations, see section Abbreviations above.

| | Study | | | |
|---|---|---|---|---|
| **Variable** | **I** | **II** | **III** | **IV** |
| Total number of species | 316 | 133 | 219 | 290 |
| ECM | 131 (41.5 %) | 133 (100 %) | - | 119 (41.0 %) |
| SM | 175 (55.4 %) [1)] | - | 212 (96.8 %) | 167 (57.6 %) |
| BM | 3 (0.9 %) | - | 3 (1.4 %) | 2 (0.7 %) |
| PM | 7 (2.2 %) | - | 4 (1.8 %) | 2 (0.7 %) |
| Total number of sporocarps | - | 14 469 | 43 102 | 87 439 |
| Total yield (g, fresh weight) | - | 159 583 | 64 791 | 167 152 |

[1)] In this thesis, six species of the litter saprophyte group have been moved to ECM and three *Omphalina* spp. (revised names *Rickenella fibula, Lichenomphalia umbellifera, Arrhenia onisca*) have been moved from the moss and peat saprophyte group to the BM species group.

All four data sets (**I**, **II**, **III**, **IV**) in this thesis were collected from the boreal forests in Eastern Finland (Fig. 1).

For study **I**, a network of permanent sample plots was established in 1980 as part of the 7th Finnish NFI (7NFI, Fig. 2). The sample plot network was denser than in the NFI and the inventory tracts were located at intervals of 4 km instead of 8 km. The area was part of the so-called Nurmes Plan (Sevola 1983) where intensive forestry (clearcutting and thinning) has been practiced in the forests, and the peatlands have been drained in a variety of ways.

A total of 596 study plots (10 × 10 m in size) were located on several forest and peatland site types in the middle boreal vegetation zone. Pine (*Pinus sylvestris)* is the dominant tree species in the semi-dry forest site types (EVT). Spruce (*Picea abies*) and, on occasion, downy birch (*Betula pubescens*) are the dominant tree species in mesic forest site types (VMT, DeMT). The EVT, VMT, DeMT and pine mires and bogs were well represented in the study area, although dry (ECT) and rich forest site types (GOMT), spruce mires and treeless bogs and fens were quite rare.

The data for studies **II** and **III** were collected from the Kitsi forest wildfire area (Fig. 2, Fig. 3). The burned areas were old managed forests that have been burned or undergone slash-and-burn cultivation four times in the last two hundred years; in 1833, 1842, 1892 and 1992 (Lehtonen and Huttunen 1997). These dry heath forests were characterized by the *Empetrum-Vaccinium* site type (EVT), with pine the dominant tree species in the area. A total of 22 permanent sample plots (10 m × 10 m) were established in the study area.

Four fire severity classes were assigned to the wildfire area based on vegetation and soil characteristics. The severity classes were termed HOT, HOT-DRY, MEDIUM and MILD. In addition, two control sites (Control-J, Control-P) were sampled, to clarify the differences in macrofungal species and species composition between the burned and unburned sites.

The data for study **IV** was obtained from experimentally burned forests that were part of the large-scale FIRE experiment (http://forest.uef.fi/jarikouki/project_fire.htm, Fig. 2, Fig. 3). In these sites, pine was the dominant tree species, although spruce, birch (*Betula pendula, B.*

*pubescens*) and other deciduous tree species were also found in the area. A factorial study design included a total of 16 sites (area of site: 2.5–3.5 ha), selected from 24 sites that were available. Three green tree retention levels (0, 10 and 50 $m^3$ $ha^{-1}$) were included, and the study sites were allocated to the burning treatments ("no fire" and "burned"). Each treatment combination was replicated twice. In the FIRE experiment, all the study sites were logged to the specific retention levels during the winter 2000–2001. Three sites from each of the three retention levels and control were burned over two consecutive days at the end of June 2001. Two of these three replicates were used in my studies.

**Figure 2.** Location of study sites. Study area for sub-studies **I**–**IV** are shown: Grey area (**I**), KITSI (**II**, **III**), FIRE (**IV**). B: Border between the southern and middle boreal vegetation zones (Ahti et al. 1968).

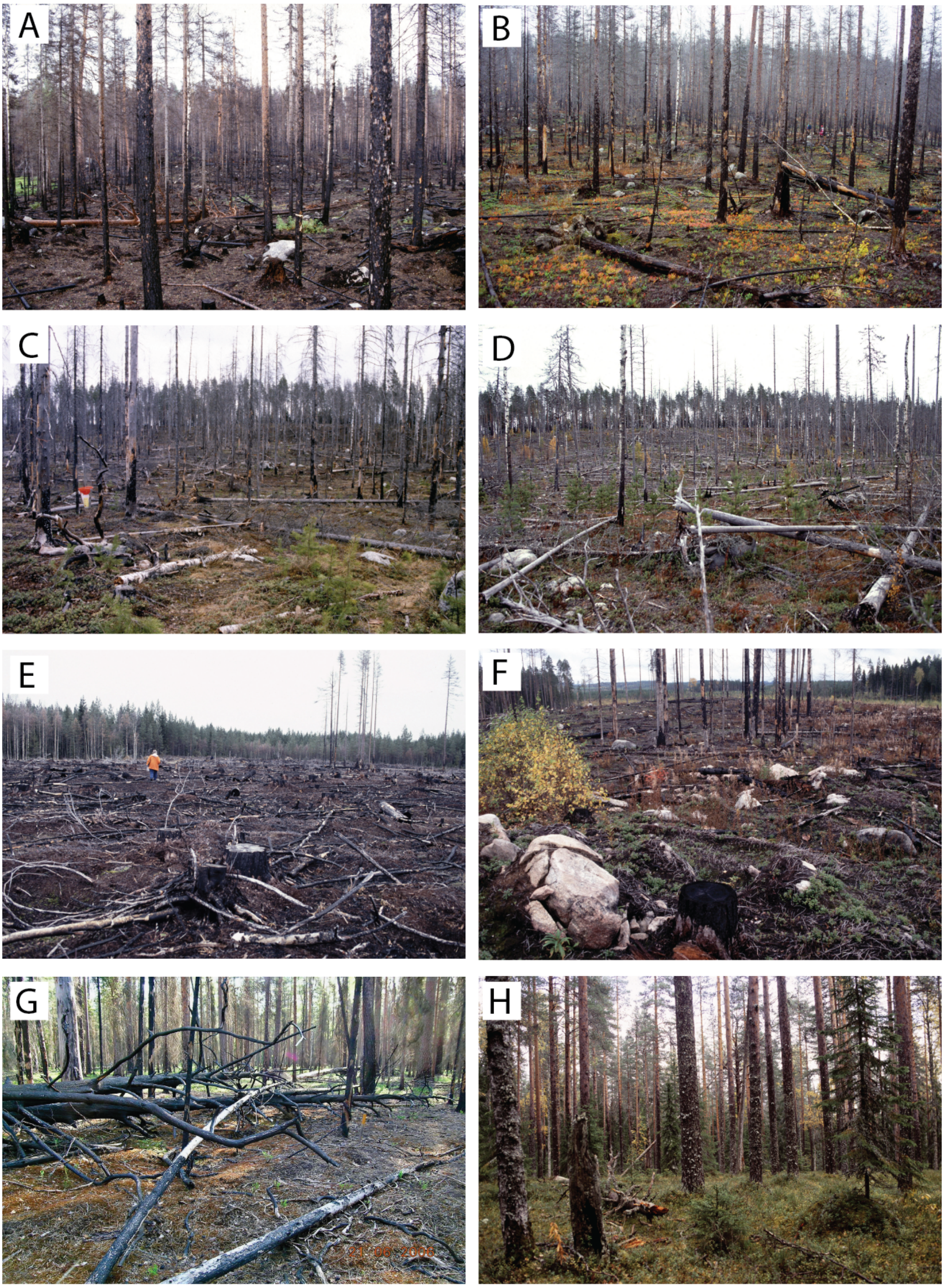

**Figure 3 A–D:** The most severely burned site (fire severity class HOT) in studies **II** and **III** in A) August 1993, B) October 1995, C) September 1997 and D) September 2000 . **E–H:** Different treatments in the study **IV**: E) burned, retention level 10 $m^3$ $ha^{-1}$, F) burned, retention level 50 $m^3$ $ha^{-1}$, G) burned, unharvested, H) unburned, unharvested. All photos are taken in 2004, except E in 2002 and G in 2006. Photos: Kauko Salo (A-F, H). Jari Kouki (G).

**Table 2.** Number of permanent sample plots, size of a single sample plot, macrofungal collection times per year, total number of visits in the sample plots and inventory years in the different studies of this thesis.

| Study | No. of sample plots | Sample plot size | Collection times per year | Total no. of visits | Inventory years |
|---|---|---|---|---|---|
| **I** | 596 | 10 m x 10 m | 1–3 | 1218 | 1981–1984 (4) |
| **II** | 22 | 10 m x 10 m | 5–6 | 1476 | 1993-2004 (12) |
| **III** | 22 | 10 m x 10 m | 5–6 | 1476 | 1993-2004 (12) |
| **IV** | 16 | 3 m x 2 m x 80 m | 2 | 128[1)] | 2001-2003 (4) |

[1)] Does not include surveys of Pezizales in June.

## 2.2 Macrofungal inventory

The main macrofungal groups studied in this thesis were ECM and SM, and biotrophic macrofungi (BM), which are lichenized macrofungi (lichen symbiosis) and comprise a relationship between algae and fungi. In contrast, PM live on plants or other fungi and cause harm or kill their hosts.

All macrofungal sporocarps (Basiodiomycota and Ascomycota) of different ages (young, medium and mature) were counted from the permanent sample plots from May to the end of October as part of the 7NFI in study **I** (note that sporocarps are termed “fruit bodies” in **I**). The surveys continued from the beginning of August to the end of October, and the sample plots were also visited in June to check for early season ascomycetes in Pezizales (in **II**, **III**, **IV**). To obtain macrofungal data in **IV**, each study site contained three mushroom inventory transects (each transect was 2 m × 80 m), located 30 m from each other, with a total surface area of 0.048 ha (**IV**). Macrofungal sporocarps were counted, individually identified and the fresh weight was measured in the field. One sporocarp counted as one observation in my study. Some macrofungi were sampled and then dried in the laboratory for further identification under the microscope. The number of permanent sample plots, macrofungal collection times per year, total number of visits to the sample plots and inventory years in the different studies are shown in Table 2.

## 2.3 Functional groups and classification of macrofungi

Four main functional groups were studied in this thesis: ECM, SM and PM in studies **I**, **III**, **IV** and ECM in study **II**. Study **III** also included BM (**III**). SM were further divided into subgroups based on their substrate affinities and resource use; the main subgroups were WAM (including AWAM) and SaM recorded on substrates other than wood, decomposing dead organic matter or living in mineral soil (**I**, **III**, **IV**).

ECM species are symbiotic with trees (Melin 1927; Smith and read 2008). Fungal symbiosis has a multitude of positive influences on tree species (Asai 1944) while the development of ECM mycelia and sporocarps depends on the photosynthesis of the living green plant or the host tree (Lamhamedi et al. 1994).

SM form a diverse group where different species live in specific substrates. In this thesis, SM included eight subgroups based on their substrate affinities and nutritional strategies (**I**, **III**, **IV**). However, the grouping inside the SM between WAM and PM was occasionally problematic since some species, e.g. *Pleurotus* spp. can be both WAM and PM. A similar problem was also faced when grouping SaM between humus (HS) and musciculous saprophytes (MS), and also between litter and humus saprophytes (**I**, **III**). Note: HS was chosen if the stem of a sporocarp was deep in the humus layer.

### 2.4 Nomenclature of macrofungi

Since the first study in this thesis was published in 1993, fungal classification has changed to some extent, some orders have been revised and the scientific names of some macrofungi have been altered.

The ECM, SM, BM and PM macrofungal species taxonomy were determined mainly following Hansen and Knudsen (1997), Knudsen and Vesterholt (2008), Hansen and Knudsen (2000). Poroid Basidiomycota were determined by Niemelä (2005), and Aphyllophoroid fungi by Kotiranta et al. (2009). Species names in studies (**II-IV**) include updates mostly according to Mycobank (2018). Exact sources for nomenclature are shown in the Methods section of each chapter (I-IV).

### 2.5 Numerical methods

TWINSPAN classification and detrended correspondence analysis (DCA) ordination was used to analyze the macrofungi in study **I**. Non-metric multidimensional scaling (NMDS) was used to visualize ECM species composition and community structure in the burned and unburned sites (**II**), and on the effects of fire severity on SM assemblages and community structure (**III**). Indicator species (IS) analysis was used to analyze the indicator species for three temporal periods in the burned and unburned sites (**III**). Study **IV** was based on a factorial experimental design, and the principal numerical method was thus analysis of variance. In addition, NMDS and indicator species analysis were used to explore assemblage compositions in **IV**.

## 3. RESULTS AND DISCUSSION

### 3.1. Fertile forests had a more diverse mycorrhizal and saprotrophic macrofungal species composition than dry and semi-dry forest site types (I).

The data comprised a total of 316 macrofungal species that were divided into four main groups: 131 ECM, 175 SM (including wood saprophytes), 3 BM and 7 PM. The most abundant genera were *Cortinarius* (27 species), *Mycena* (19), *Russula* (16), *Lactarius* (15) and *Tricholoma* (10).

Annual climate variation was large in all the study areas during the inventory years 1981–1984. Weather conditions were favorable for the growth of macrofungi in 1981, but the growing season in 1982 was very dry and hot, and as a result the total number of macrofungal species in that year was very low. The inventory years 1983 and 1984 were normal in terms of weather conditions.

The fertile forest site types had a more diverse composition of mycorrhizal and saprotrophic macrofungal species than the dry and semi-dry forest site types. The pristine pine bogs had less macrofungi than recently drained or transitional drained pine bogs.

I was able to determine seven distinct macrofungal communities typical of a particular forest and peatland site type in dry, semi-dry and mesic boreal forests and peatland sites. In 1981, these macrofungal communities were characterized by 5–6 of the most abundant plant and macrofungal species, based on TWINSPAN classification and DCA ordination.

The ECM and SM species composition differed from each other in the dry, semi-dry and mesic forests in both spruce mires and pine bogs, as a consequence of the tree, shrub and dwarf-shrub species and vegetation composition in the field and ground layers.

Sampling covered a number of old spruce forests and the volume of dead wood was on average 5 $m^3 ha^{-1}$. Rare and Red-listed agarics and AWAM species were absent. Pyrophilous species were not found, except for one pyrophilous agaric *Myxomphalia maura*, (former name *Fayodia maura*) that was found on burned ground in a campfire site (**I**).

Macrofungal species diversity was highest in the mesic VMT/DeMT site (total of 102 macrofungal species), followed by the semi-dry forest site EVT (72) and the dry forest site ECT (59). Mixed sample plots contained elements of both forest and peatland site types or two different forest and peatland site types in one sample plot and for that reason they did not form their own groups.

ECM species from the genus *Cortinarius, Lactarius*, *Russula*, and SM species from the genus *Mycena* dominated in all forest site groups but species composition within genus differed from each other between the dry and semi-dry mesic heath forest groups.

### 3.2 Non-ditched pine bogs had less macrofungi than recently drained or transitional pine bogs (I).

Four macrofungal community groups could be determined in the peatland site types. According to the fertility classes, the non-ditched pine bog group (peatland site types TR, RaR, LkN) had less macrofungi than recently drained or transitional drained pine bogs. Many typical saprophytes of pristine bogs (*Galerina paludosa, Hypholoma elongatum* and *Lyophyllum palustre*) lived in *Sphagnum* communities.

The macrofungal species diversity was higher in the recently drained or transitional drained spruce mires (67 macrofungal species), pine mires (59) and bogs (58) compared to the pristine pine bogs (13 species). This reflected the diversity of tree species, dwarf-shrubs, *Sphagnum* spp. and heath mosses in these sites.

In the drained pine mire (PsR) and bog (TR, IR) groups, *Lactarius rufus* was the main ECM species exhibiting large yields here and also in the drained and fertilized pine bogs (Salo 1979). Drainage improved the height growth of the pines and many ECM species benefitted from these improved conditions after ditching, and some saprophytes (*Mycena* spp.) were abundant among *Sphagnum* species and heath mosses.

### 3.3 Fire had a mostly positive effect on ECM species but high severity fires had negative effects on species richness and post-fire succession of ECM species (II).

I analyzed the long-term effects of wildfire on ECM assemblages. I focused on the impact that fire severity variation had on macrofungal assemblages in Scots pine (*Pinus sylvestris*) dominated forest; 22 permanent sample plots with four different fire severity classes in burned and unburned control sites were assessed between 1993–2004.

A total of 133 ECM species and 14,469 ECM sporocarps were sampled. Total fresh weight was 159,583 grams in 1993–2004. The most abundant genera were *Cortinarius* including var., cf., s. lato and coll. species (44 species) followed by *Russula* (16) and *Tricholoma* (12).

Fire severity had a negative effect on ECM species richness and community composition. ECM species diversity was highest in the intermediate fire sites; almost three times greater in comparison with the high-severity fire sites. High-severity wildfire may cause decadal long changes in ECM assemblages. My results also showed that wildfires can enhance ECM diversity and the production of some edible mushroom species but only if the fire severity is not too extreme.

The importance of long-term monitoring of ECM and SM species, as well as macrofungal sampling during the whole growing season, was evident in this long-term study. Most macrofungal surveys have a limited time-span that typically last only a few years, and for this reason the number of macrofungi has probably been underestimated in short-term studies (Mueller and Schmit 2000; Abrego et al. 2016; Frøslev et al. 2019). My results showed that 68 % of all ECM species over a 12 year-period were rare or very rare, which confirms that sporocarps of ECM must be monitored for a decade or more in order to reveal the main successional patterns.

### 3.4 The yield of a number of ectomycorrhizal edible mushrooms was high in medium-burned sites (II).

Edible mushrooms and wild berries are important non-wood forest products in Finland. For example, the value of the commercial mushroom yield in 2000 was €21.4 million (Salo 2011). The list of recommended commercial mycorrhizal and saprotrophic mushrooms includes approximately 40 species, depending on how the species are assigned to the *Boletus* and *Leccinum* groups, the genus *Armillaria*, the species *Hydnum rufescens* coll. (new name *Abortiporus biennis*), *Morchella* spp. and *Tuber* spp. (Evira 2013).

According to my results, sporocarp production in some edible mushroom species (*Suillus variegatus, Russula paludosa* and *Leccinum vulpinum*) increased in medium- and mildly-burned sites, with *Lactarius rufus* yield the highest (130 kg ha$^{-1}$) in fresh weight. This is well above typical values: in the 8th NFI the average fresh weight yield of *L. rufus* in various forest site types was 19.3 kg ha$^{-1}$ (Salo 1993).

### 3.5 Fire severity affected SM species richness and composition, and fire always increased macrofungal diversity in comparison with unburned control sites (III).

A total of 212 SM, 3 BM, 4 PM species and 43 102 sporocarps of SM were gathered and identified. Total fresh weight was 64 791 grams.

The SM group was divided into two main groups, based on substrate affinities and resource use. The WAM group (including AWAM species) contained 118 species and the SaM group contained 94. The latter were divided into 8 subgroups in substrates other than wood, decomposing dead organic matter or living in mineral soil. The 3 species in the BM group consisted of 2 lichenized macrofungi (*Rickenella fibula, Lichenomphalia umbellifera*) and *Geopyxis carbonaria*, which lived in mutual symbiosis with mycorrhizae. The 4 species of PM cause harm to host tree species. The most abundant genera were *Mycena* (17 species) and *Pholiota* (9), followed by *Clitocybe* (7) and *Gymnopus* (6).

Wildfires result in tree mortality, and also burn and char organic matter. Thus, fires increase the prevalence of new habitats and resources for decomposers. I found that wildfire severity increased SM species richness, composition and sporocarp production, and also affected the SM assemblage structure. The number of SM sporocarps were substantial during the first four inventory years in severely burned sites, although the number of sporocarps declined and SM assemblage rapidly changed in subsequent post-fire years.

### 3.6 The succession of indicator species and fire-associated pyrophilous species in burned humus was rapid compared to the succession of aphyllophoroid and other wood-associated macrofungi in burned wood (III).

The succession of fire-associated pyrophilous and facultative pyrophilous species was rapid on the burned humus one year after wildfire. In contrast, the appearance of AWAM and other WAM species in burned wood was slower. After three years, the number of pyrophilous species had declined significantly in the different fire severity classes, and the decrease in AWAM species was slower than in the pyrophilous species. I did not observe pyrophilous agarics and ascomycetes in the unburned control sites.

Many pyrophilous IS (e.g. *Myxomphalia maura* (HS), *Pholiota highlandensis* (HS), *Galerina carbonicola* (HS), *Rhizina undulata* (PM), *Geopyxis carbonaria* (BM)) were abundant after wildfire in the burned sites. Three years post-fire, the number of IS had decreased. The IS were early colonizers and many of them were classified as pyrophilous species in burned humus sites. The AWAM species and agarics formed a diverse group of species on fallen and standing trees, tree components or in softwood.

Based on my observations, fine woody debris (FWD), in addition to CWD, can be viewed as a favorable substrate for AWAM species. Only six AWAM species were found in the control sites and one AWAM species was recorded in both the charred wood and unburned control sites. The AWAM species were positively correlated with the volume of dead wood. The effects of fires on AWAM species have been documented previously (e.g. Penttilä et al. 2013; Suominen et al. 2015), but fire studies on SM species, especially pyrophilous species, are scarce.

### 3.7 Forest disturbances modify functional groups of fungi in young successional forests – clear-cutting and fire lead to different fungal assemblages (IV).

Study **IV** included 16 sites where burnings and timber harvests were monitored between 2000–2003. In total, we found 291 species and counted 87 439 fungal sporocarps with a total fresh weight of 167 152 grams.

Macrofungi were surveyed 2 times a year in each of the 16 sites. They were divided into ECM, SaM and WAM groups. Fire (prescribed burning) and timber harvests had a major influence on macrofungi in the three post-fire years (2001–2003).

However, the results show that fungal groups respond in different ways to major disturbances in boreal forests. The number and biomass of ECM species collapsed in all harvested sites. Unharvested sites maintained their ECM assemblages, and fire had no discernible effect on ECM populations on these sites. The number and biomass of SaM species other than WAM decreased after fire in unburned sites and was at the same level in the two post-fire years in burned sites. In the final monitoring year, the number and biomass of wood-decaying fungi began to increase in the burned and unburned sites.

My results show that early successional post-disturbance forests contribute to the maintenance of forest biodiversity, especially specialist SaM species. However, the type of disturbance (fire or harvest) affects fungi in different ways. Understanding the assemblage dynamics of decomposers and other fungi is crucial when estimating how changes in forest disturbance regimes may affect nutrient and C cycling, as well the maintenance of fungal diversity in forests, including managed forests.

### 3.8 Conclusions and management implications

My thesis leads to conclusions that also have relevance for forest management:

1. Macrofungal species form distinct assemblages in forests and peatlands, which follow the composition of the vegetation in the site. Silvicultural factors, mainly clear-cutting, forest stand age and ditching in peatlands, strongly affect macrofungal richness and composition. Forest site types with development classes of tree stands and peatland site types in different fertility classes are characterized by ectomycorrhizal and saprotrophic macrofungal communities typical to each habitat.
2. Tree species composition of a forest stand, the age of the stand, and the density of the trees affect the occurrence and populations of macrofungi. Young forest stands have distinctive macrofungal communities, especially after fire. Assemblages also include distinct pyrophilous communities. Prescribed burnings can be used to maintain similar assemblages as wildfires, which is why prescribed burnings are recommended in managed forests.
3. Logging and other silvicultural measures also affect the edible mushroom species that can provide a significant income for Finnish households. Prescribed burning and retention can alleviate the negative consequences of intensive forestry on the yields of ectomycorrhizal macrofungi, including some edible mushrooms.

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